THE
AMERICAN NATURALIST

VOL. L. *August, 1916* No. 596

THE FORM OF EVOLUTIONARY THEORY THAT MODERN GENETICAL RESEARCH SEEMS TO FAVOR

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Nature produces those things which being continuously moved by a certain principle contained in themselves arrive at a certain end.

—Aristotle.

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I. GENERAL STATEMENT OF THEORY OF EVOLUTION

THE history of evolution, all will agree, has been from the less specialized to the more specialized. The prevailing view is that this greater specialization has been achieved by adding qualities one by one to the less specialized until there has become built up through the ages so complex structures as the higher types of organisms. Organic evolution, from this view, has proceeded along the same lines as the evolution of an old English manor

house through the accretions of successive generations; or is like some medieval cathedral to which each generation has added some sculptures, some stones to the steeple, some new stained-glass windows. Organisms, the theory runs, began simple,—they varied, why or how no matter; variation is given and is in all directions. Positive variations toward greater complexity were usually advantageous and individuals showing such elbowed out of existence their less-favored cousins and established a new and higher level from which evolution might proceed.

This view has certain resemblances to an old view of ontogeny. The embryo is simple. Food is added and food makes this part and that grow. Why only certain parts grow in the presence of food and not all—the differential nature of growth—that is *given*. It is the nature of the organism that all parts should not grow equally; but the essential thing is that food and water and heat are the things that add parts and make the embryo larger and more complex.

This view of development has, I think it will be admitted, now become generally abandoned. To-day we recognize rather that the egg or embryo is not so simple, but that, on the contrary, it has wrapped up in it all of the potentialities that are eventually realized; potentialities that will be realized, however, only if conditions of life (food, water, heat, etc.) are appropriate.

The alternative view of evolution, like the modern view of embryonic development, lays more stress on the internal factors of evolution. It postulates that the primitive organisms, like the eggs, are not so simple as they look but have a molecular constitution of great complexity; and, just as the egg has a mechanism by virtue of which (under favorable conditions) it develops, so the ancestral protoplasm had a mechanism by virtue of which (under favorable conditions) it *evolved*. We do not know much about the specific molecular machinery that determines the specific nature of differential growth, but

we have reason to think that it is located chiefly in the nucleus. Similarly we are ignorant of the specific nature of the machinery that determines phylogenetic variations, but we have reason to think that it is located in the germ plasm and that the karyokinetic phenomena, especially the movements of chromosomes at and around the time of fertilization, have a great deal to do with such phylogenetic change. But as the egg with its given internal mechanism of development under adequate external conditions will develop into the specific adult form, so the primitive germ plasm with its internal mechanism of evolution under adequate external conditions has developed into all those forms or kinds of germ plasm that are responsible for the great variety of present and past organisms. Just as the egg-nucleus contains probably fewer kinds of molecules, but each more complex, than a nerve cell, *e. g.*, of the adult, so the ancestral form of protoplasm probably contained fewer kind of molecules each more complex than the derived forms. The derived forms, conversely, have more kinds each of simpler constitution.

In this view (if we may let our imagination picture the consequences) the foundation of the organic world was laid when a tremendously complex, vital molecule capable of splitting up into a vast number of kinds of other vital molecules was evolved! The capacity for thus splitting off molecules determines the possibility of production of the organic species with their vast number of characteristics.

It is to be kept in mind, however, that the number of genes is probably less than the number of elementary species. For numerous elementary species differ by only one or two genes and in many cases the species differ only in new *combinations* of the same set of genes.

This theory of evolution is not new; it is that briefly expressed by Bateson in his Australian address; it is very clearly expressed by Hagedoorn in Roux's "Vorträge" and has received the support of Lotsy (1913). It

is, however, essentially Nägeli's theory of evolution from within by virtue of a perfecting or progressive tendency, in support of which Nägeli himself draws the parallel between embryology and evolution. It has certain points of resemblance to Eimer's orthogenesis, but differs from it tremendously in that Eimer thought evolution was directed by the external world and that there were summed in the germ plasm the impressions of that world received in successive generations. Huxley was inclined to accept the theory of internal factors in evolution. He says:

> I apprehend that the foundation of the theory of natural selection is the fact that living bodies tend incessantly to vary. This variation is neither indefinite, nor fortuitous, nor does it take place in all directions, in the strict sense of these words. . . . A whale does not tend to vary in the direction of producing feathers, nor a bird in the direction of developing whalebone.

Mivart and many others have long contended that evolution is due to *internal* factors. Their views are in accord with Aristotle's.

Finally, I may close this section by quoting a simile from Bergson, as translated by Mitchell.

> The evolution movement would be a simple one, and we should soon have been able to determine its direction, if life had described a single course, like that of a solid ball shot from a cannon. But it proceeds rather like a shell, which suddenly bursts into fragments, which fragments, being themselves shells, burst in their turn into fragments destined to burst again, and so on for a time incommensurably long. We perceive only what is nearest to us, namely, the scattered movements of the pulverized explosions. From them we have to go back, stage by stage, to the original movement.
>
> When a shell bursts the particular way it breaks is explained both by the explosive force of the powder it contains and by the presistance of the metal. So of the way life breaks into individuals and species. It depends, we think, on two series of causes: the resistance life meets from inert matter, and the explosive force—due to an unstable balance of tendencies—which life bears within itself.

II. Support for the Theory from Collateral Fields

The view that the course of evolution (like the development of the individual) is chiefly determined by internal

changes receives support from various collateral fields of investigation.

1. First, from *embryology,* by analogy. The development of the embryo is directed from within. The process of development is one of specialization; a great number of tissues is produced but these tissues have lost the capacity, which the embryo has, of producing all kinds of tissues. Development is essentially an irreversible process just as evolution is, and for the same reason—that a fragment can not produce the whole. The adult individual is more complex than the fertilized egg, yet the egg has greater potentialities than any tissue-cell has. Regeneration depends on the presence of embryonic, *i. e.,* non-tissue, cells lying latent amidst the tissue cells. The greater complexity of the adult as a whole over the egg does not hold for a given tissue cell—*that* is *less complex* than the egg. The complexity of the adult is due to the fact that there are in the body many kinds of tissue cells, each simple, while the egg is just one kind of cell—but very complex in constitution. Similarly, we may infer that while the vast number of *kinds* of germ plasms in the higher organisms, differentiated in respect to their chromomeres, contrasts with the condition in the protista, it is probable that each chromomere of the protista is composed of much more complex organic molecules or molecule complexes.

2. Another mass of evidence for this theory is supplied by *paleontology.* By this science are offered extensive series showing: (*a*) the usual beginning of a new character as a simple, often inconspicuous trait, (*b*) the increase of variety in the course of evolution of a phylum ending in great outburst of extreme and bizarre forms immediately preceding the extinction of a phylogenetic line; (*c*) the irreversibility of the process of evolution; and (*d*) parallelism in evolution of allied lines.

(*a*) *The Simple Beginning of a Trait.*—The early history of a number of spinose groups of species shows (Beecher, 1898) that each group began its history in

small, smooth or unornamented species. The septæ of ammonites begin simple and later evolve their extraordinary foldings. The horns of titanotheres "have excessively rudimentary beginnings phylogenetically, which can hardly be detected on the surface of the skull" (Osborn, 1912, p. 253). Also, these "rudiments arise independently on the same part of the skull in different phyla at different periods of geological time."

(*b*) *The History of Progressing Phylogenetic Development.*—While paleontologists have no knowledge of germinal conditions they can study the course of evolution of a particular character through a lineage comprising thousands of generations. Paleontologists are agreed that characters tend to become more and more complex. So Beecher (1898, p. 354) writes:

> The smooth, rounded embryo or larval form [terms used in the phylogenetic sense] progressively acquires more and more pronounced and highly differential characters through youth and maturity. In (paleontological) old age, it blossoms out with a galaxy of spines, and with further decadence produces extravagant vagaries of spines. So in the titanotheres the horn rudiments evolve continuously, and they gradually change in form, . . . they finally become the dominant characters of the skulls, showing marked variations of form in the two sexes.

The saber-toothed and other tigers gained canines that they could not use. The mollusc, *Hippurites,* gains a shell a foot thick. In the Labyrinthodonts the infolding of the teeth has been carried to an extraordinary degree, etc. These are illustrations merely of what is said to be a general rule. F. B. Loomis[1] writes of it under the head "Momentum in Evolution."

(*c*) *The Irreversibility of the Process of Evolution* has been often remarked upon. It leads to exaggerated developments in one direction; lateral and backward variations are relatively uncommon.

Thus, the horse has shown divergent lines of evolution but none returning to the four-toed ancestral type. The ammonites went from simpler forms of septum to more and more complex without reversal, except at the very end of their phylum. D. Rosa says:

[1] AMER. NAT., 39 (1905).

> An organ which in the course of its phylogenesis once disappears has disappeared for ever. . . . Not an exception is known to the rule.

Even an organ once rudimentary, like flying in some ground birds, never returns to full activity. A striking example of dropping out is that of cilia in Arthropods; which, ubiquitous in other groups of animals, are in this group gone throughout; they fail to develop even in spermatozoa. Toward the end of the process of evolution, a character tends to break up into a great number of new characters. These usually affect a certain organ, like the suture of the ammonites, and precede extinction of the phylum. We may say that the number of genes has become, through fractionation, so great that the resulting complexity or the resulting extremes of development of a trait are prejudicial to the development of the organism.

(*d*) *Parallelism of Evolution in Allied Lines.*—This parallelism was recognized by Darwin who writes:

> The principle formerly alluded to under the term of *analogical variation* has probably in these cases often come into play; that is, the members of the same class, although only distantly allied, have inherited so much in common in their constitution, that they are apt to vary under similar exciting causes in a similar manner; and this would obviously aid in the acquirement through natural selection of parts or organs, strikingly like each other, independently of their direct inheritance from a common progenitor.

Of such parallel variations Osborn (1915, p. 216) speaks as follows:

> Similar rectigradations may arise in all the descendants of similar ancestors at different periods of time; they always give rise to parallelism or convergence between the members of related phyla.

Illustrations of such are afforded in many paleontological monographs.

3. Another line of evidence for the theory of the primacy of internal factors of evolution is found in *experimental breeding.* This evidence appears in the facts (*a*) that many mutations begin small and can be rapidly evolved into highly developed characters, (*b*) that similar variations appear in related organisms, (*c*) that

mutation is limited to certain lines and (*d*) that experimental evolution seems *chiefly* due to dropping out of genes.

(*a*) That *characters often arise as rudiments* and only in the course of generations realize their full potentiality is a well-known experience of breeders. Thus De Vries[2] states that the double *Anemone coronaria* was produced by the owner of a nursery who, observing in his beds a flower with a single broadened stamen, saved its seeds separately and in the succeeding generations procured beautifully filled flowers. By appropriate matings Castle succeeded in 5 generations in getting much better expressed polydactylism in guinea pigs than he had at the outset. Dr. F. E. Lutz (1911) found a slight abnormality of venation in the fruit fly, *Drosophila ampelophila*. By in-breeding abnormally veined flies and selecting as breeders the extremely abnormal flies he eventually secured in the later generations some highly abnormal individuals. From a hen that showed only a slight extension of the web between certain toes I succeeded in breeding a race of profoundly syndactyl descendants.

(*b*) That *mutations* (*"saltations"*) *run in parallel lines* in related species is well brought out in a table given by Osborn (1912, p. 191), which I reproduce here with certain modifications.

That each germ plasm can vary only within certain limits and that related germ plasms show only a limited number of variations and the same in the different species indicate that variations of the specific rank are not determined by anything outside the organism, but by the very nature of the organism. Thus, the rabbit shows in its coat color the agouti coloration, and so does the guinea pig. From this in the guinea pig have arisen yellow, chocolate, black, albino and other colors; and a similar series has been obtained for rabbits. The guinea pig has produced an angora coat and so has the rabbit,

[2] "Species and Varieties," p. 491.

COMPARATIVE TABLE OF SALTATIONS

	1	2	3	4	5	6	7	8	9	10	11
	Man	Horses	Cattle	Sheep	Deer	Pigs	Dogs	Cats	Rabbits	Guinea Pigs	Mice
1. Proopic brachycephaly, abbreviation of face	..	..	×	..	..	..	×	..	..	..	..
2. Sudden development of horns on hornless races	..	×	..	..	..	..	..	..	×	..	..
3. Absence of horns on horned races	..	..	×	×	..	..	..	..	..	..	..
4. Jaw appendages	×	..	..	×	×	..	..	..	..	..	..
5. Taillessness, absence of caudals	×	×	..	×	..	..	..	×	..	×	..
6. Short-leggedness, or limb abbreviation	×	..	×	×	..	..	×	..	..	..	..
7. Consolidation of paired hoofs, syndactylism	×	..	×	..	..	×	..	..	..	..	..
8. Polydactylism	×	×	×	×	×	×	×	×	..	×	..
9. Epidermal thickenings	×	..	×	..	..	..	..	..	..	..	×
10. Mottled skin markings	×	×	×	..	..	×	..	..	..	..	..
11. Excessive hairiness, or length of hair	×	×	×	×	..	..	×	×	×	×	..
12. Hairlessness, entire absence of hair	×	×	×	..	..	..	×	..	..	..	×
13. Excessively fine or silky hair	×	..	×	×	..	..	..	×	×	..	×
14. Reversed hairs	×	..	×	..	..	..	..	..	..	×	..
15. Curled-hair	×	×	..	×	..	..	×	..	..	..	..

the cat, the dog, the goat, the sheep (Lincoln) and others. So in different species of *Drosophila,* I am informed by Dr. C. W. Metz, the same mutations occur—of course, without any relation to environment.

In a strain that has produced a mutation once we are apt to find the same mutation a second time. Thus De Vries states that the peloric toadflax does not set seed in nature, yet it occurs repeatedly in a given locality and even in distant localities. We conclude there is something in the structure of the germ plasm of the toadflax that permits a wholly useless, and indeed not naturally perpetuated, mutation to occur easily. Similarly, doubling of the floral parts occurs again and again in wholly unrelated species; often combined with complete sterility. Again, poultry sometimes show a great extension of the web between the toes. This occurs chiefly between digits III and IV, exactly where the syndactyl web occurs in man and where it occurs in wading birds that have only a single web between the toes—of which 8 genera might

be named. So far as I know, a marked extension of the web between digits I and II has never been observed; between II and III it is relatively rare; again, between IV and V it has, so far as I know, not been noted in mammals.

(*c*) *Variation is Not Indefinite and Multifarious.*—The case of syndactylism in poultry well illustrates the general principle of the *limitation* of mutation to particular narrow lines; and this is commonly the case. Thus, Dr. J. A. Harris has examined himself and with the assistance of others over 1,000,000 bean seedlings, and while extraordinary variations have been found, yet in the later hundreds of thousands no new ones have appeared; nevertheless, the possibilities in leaf form, variegation, etc., if we may judge from books on plant teratology, are by no means exhausted. And when we contemplate the variety of form assumed by first leaves in different species, is not the constancy in the form in beans striking evidence of the narrowness of variation and its restriction to certain lines?

(*d*) *Evolution by Loss of Genes.*—Finally, it has long been recognized that an extraordinarily large proportion of the mutations we meet with are recessive to the wild type. Castle has noted this of rabbits and guinea pigs[3] and Morgan has noted it in the case of *Drosophila.* In my work with poultry I was not impressed with it, as taillessness, polydactylism, syndactylism, white color of the Leghorn, rose comb, etc., are dominant mutations. Still, other genetics work (Baur, Shull and many others) is strengthening the conclusion that current evolutionary changes under observation are chiefly due to the dropping out of genes, and this supports the theory that evolution is proceeding largely by the loss of genes. However, the fact of dominant mutations can not be derived. Take, for instance, foot abnormality. Here a disturbing factor has appeared in the organism that was not there before. There is no *a priori* reason for doubting that the break-

[3] "Heredity," p. 86.

ing up of one of the genes that makes for the normal foot might have a residuum that positively interferes with the operation of other foot-forming factors.

The genetical studies also accord with other evidence as to the general irreversibility of evolution. We see that when a population contains only a recessive trait it is impossible by breeding inside that population to get back the dominant allelomorph. From a pure blue-eyed population we do not get back the primitive brown-eyed condition.

It might be thought that if evolution proceeds chiefly by loss of factors it would tend to simplification rather than increase of the number of factors. It seems probable, however, that the loss is not merely of a whole gene, but of some part of it; a fractionation, as it were, by which the gene becomes altered or split up into two or more. For example, it is probable that in man the loss of a gene (or a part of one) releases special nervous states, as, for instance, that in which musical combinations run through the brain, or numerical relations are rapidly worked through, etc. Thus the *general* result of experimental work in genetics gives support to the view of evolution by loss of genes and by their fractionation.

4. *Evidence from Evolutionary Changes in the Inorganic World. Radiation Studies.*—The view that evolution is primarily by internal changes receives unexpected support from the recent discoveries concerning the evolution of the elements. It is now well known that the element, uranium, under certain conditions of temperature, etc., undergoes a spontaneous change into ionium, ionium into radium, radium into polonium, an essentially lead-like substance. Similarly, thorium passes through mesothorium and radiothorium. Indeed, in a particular series, side branches may be given off; thus polonium is not derived directly from radium, or from radium *C*, but from one form of radium *C* called radium C_1. Indeed, "radiums" of different sorts, called radium *A*, radium *B*, radium *C*, are recognized and the atoms of these differ

from one another by, probably, one electron lost from each successive stage of the series. The series is thus shown graphically by Sieveking (1913):

$$\text{Ra} \rightarrow \text{Em} \rightarrow \text{Ra}A \rightarrow \text{Ra}B \rightarrow \text{Ra}C_1 \begin{cases} \rightarrow \text{Ra}C_2 \\ \rightarrow \end{cases} \rightarrow \text{Ra}D \rightarrow \text{Ra}E \rightarrow \text{Ra}F$$

III. CERTAIN CONSEQUENCES OF THE THEORY

1. The acceptance of this theory requires a special *explanation to account for adaptation.* Eimer's theory of orthogenesis posited the direct action of environment on the germ plasm, a view which wider knowledge of facts does not support. It follows naturally from the hypothesis that new traits bear, at first, no relation to environment any more than the polonium that is derived from the uranium does. Darwin recognized that variations were not necessarily adaptive in their origin; also that it was not necessary that they should be adaptive in order to survive. Darwin says:[4]

> We clearly see that the nature of the conditions is of subordinate importance in comparison with the nature of the organism in determining each particular form of variation.

How then is adaptation brought about? Strictly, we may say adaptation is not the thing that is brought about, but rather absence of non-adaptiveness. Such adjustment as we find is, doubtless, only such a residuum of variants as has not proved incompatible with conditions of existence. Two kinds of variations may survive: (*a*) Those not incompatible with the conditions of the present environment and (*b*) those which, while incompatible with present environment, are not incompatible with some other environment into which the species may migrate.

2. *Relation to the Rôle of Selection in Evolution.*— There is going on to-day a great discussion as to the importance of selection in evolution. How does the matter look from the standpoint of this theory.

First, all are agreed that nothing has importance for

[4] "Origin of Species," p. 9.

evolution of the race except what modifies the germ cells, because they are all that goes from one generation to the next. However, we learn little or nothing about the potential traits of the germ cells by looking at these cells. Our knowledge of their hereditary composition depends upon the traits shown by the individuals that develop out of them. We may infer the genotype by observing the phenotype. But the phenotypical condition of a person is a more or less imperfect index to the genotypical condition of that person. The soma is an imperfect index to the germ plasm. The difference between the two schools, one asserting, the other denying the value of "selection," is based primarily upon the reliance placed on the sufficiency of this index. Castle says, in effect, the somatic condition of my rats in respect to the coat-pattern is so good an index of their germinal condition that whenever I select rats for a quality of the pattern I am selecting them very closely for the corresponding quality of their germ plasm. Pearl says, in effect, in poultry the egg-laying capacity of the hen is hereditary; yet it is so poor an index of her germinal idiosyncrasies in this respect that an individual with the somatic characters of high laying is no more apt to have the genes for high laying than an individual with the somatic character of low laying. Pearl says to make progress I must select for breeders those which have proved their germinal quality by belonging to a race of high layers. If the various sisters and daughters of the hen are high layers, that is more important than the egg-laying performance of the one individual, merely.

It seems to me that the whole question is a pragmatical one. If the somatic condition of a trait is a good index of germinal conditions, in any case progress can be made by selecting the soma in that case; if the soma is an inadequate index, then little or no progress will be made by selecting the soma. We know this by breeding experience. If we select parents because of absence of pigment in skin or eye, we select also a germ plasm devoid of the

capacity for forming such pigment. If we select parents because they have medium-brown hair we get offspring with blond or golden or red hair even, and it would take a long time to get a pure brown-haired race by this method of selecting. If the trait that we are trying to improve is very sensitive to environment, then the somatic conditions will be a very bad index of the germinal; but if not sensitive, the somatic may be a good index of the germinal. Thus, since in the fruit fly the number of bristles varies closely with food conditions, selection of breeders merely on the somatic state will not lead to much, if any, genetic progress.

The question of the potency of selection in nature comes back to the matter of value of the soma as an index of the germ plasm. If blue eye color affords insufficient protection from tropical conditions elimination of the blue-eyed individual kills off blue-eyed plasm and with each death the race is rapidly purified. But there is a limit to the process because brown eyes are preserved equally whether the germ plasm does or does not carry the blue-eyed condition. As there are twice as many simplex as duplex brown eyes, the complete elimination of the blues will not be brought about quickly.

When, therefore, we hear a breeder say: "I made this character by *selection*" what he really means is: Somatic variations in the desired direction were afforded; there was a large correlation between somatic and germinal conditions, so that I was able, merely by choosing as breeders individuals showing the desired trait somatically, to get a race with the determiners of the character pure, or practically pure, in the germ plasm.

One other difference of opinion there seems to be between selectionists and the others. Castle evidently doubts if factors for characters are always discrete and do not change. He is inclined to hold that there may be genes which vary *pari passu* with a variation of a "unit character" and in somewhat the same degree. This view seems to be quite in accord with an expectation that

is based on experience, that traits shall be found the germinal bases of which are undergoing current evolutionary changes through loss of genes or through fractionation. And it is in accord with expectation that mutations shall reveal themselves just at the extreme of a series as Castle's plus mutation revealed itself. Others are inclined to think that the varied color pattern of Castle's rats is really determined by several factors (restrictors or extensors of the gene for "hoodedness") which were all in his race of rats at the beginning of his experiment. Upon one point all geneticists are, however, agreed—that we must interpret all of our results in terms of genes alone.

One other bearing of the orthogenetic theory deserves to be pointed out. If the germ plasm is capable of undergoing a spontaneous mutation which is the main source of evolutionary change, this fact would seem, at first blush, to indicate the futility of trying to control genetic change experimentally, except by the selection of germ plasms. Naturally, under these circumstances our effort would be limited to what nature affords. However, we do not yet know enough to put these limits on "experimental evolution." There is some evidence, although not as critical as might be wished, that the germ plasm is not beyond the reach of modifying agents. At least we must continue experimental efforts in that direction.

IV. Summary

A theory of evolution that assumes internal changes chiefly independent of external conditions, *i. e.*, spontaneously arising, and which proceeds chiefly by a splitting up of and loss of genes from a primitively complex molecular condition of the germ plasm seems best to meet the present state of our knowledge.

Such a theory receives support from various fields.

1. From ontogeny, where the differentiated end stage is derived from a relatively undifferentiated, but probably molecularly complex egg.

2. From paleontology, where the history of the phylum seems governed by internal laws.

3. From experimental breeding where progress is afforded only as internal changes permit.

4. From analogy, with evolution in the inorganic world, so far as may be inferred from the studies on the "rare earths."

Such a theory makes clear that success in "selection" depends on rate and amplitude of internal change and ability to judge of germinal from somatic conditions.

It renders less hopeful (but not hopeless) the prospect of being able to control completely by experimental methods evolutionary change.

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COMPARATIVE RAPIDITY OF EVOLUTION IN VARIOUS PLANT TYPES

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DURING the course of evolutionary development among the higher plants certain groups have evidently altered with such exceeding slowness as to retain their ancient constitution practically intact for very long periods; whereas others, by their more rapid accumulation of heritable variations, have during the same time undergone far-reaching changes and become developed into new and radically dissimilar types. These differences in the rate of evolution are apparently due in part to differences in mutability, in the extent to which hybridization has occurred, in the degree of diversity presented by the environment or in the keenness of the struggle which is waged for survival. The purpose of the present paper is to call attention to still another factor which seems to be of much importance in determining the rapidity of evolutionary change among plants, namely the length of the generation or period from seed to seed.

The time necessary for the attainment of reproductive maturity among plants is definitely correlated with the growth-type to which a species conforms. Trees are very slow to mature, some arriving at an age of eighty years or more before their first flowering time and very few indeed, under natural conditions, fruiting before the tenth season. The scanty available observations seem to indicate that the average period from seed to seed in arborescent forms is in the vicinity of twenty years. Among shrubs the generations are decidedly shorter, varying usually from three to ten years. The herb is the most rapidly maturing of all, a single year sufficing to develop seed in an annual and but two (rarely more) in a biennial or perennial. Most herbaceous species will thus have

from fifty to one hundred generations a century, most shrubby ones from ten to thirty and most trees only four or five. The degree of variability and other factors being equal, therefore, one would expect changes to accumulate much more rapidly and evolutionary progress consequently to be much faster among herbs than among woody plants. Is there evidence that this is actually the case?

In an attempt to obtain such evidence an analysis as to growth-habit was first made of the endemic portion of the floras of several regions. Upon the biological isolation of an area the new varieties, species and genera of plants which gradually take their origin in its flora are necessarily limited in their distribution to the region in question, or are "endemic" in it; and these local types will evidently be produced first and in greatest abundance by those elements in the flora which are changing most rapidly. Consequently that particular growth type which is found to predominate among such endemic forms may justly be regarded as the one whose members are undergoing the most rapid alteration. In an analysis of the endemic element in any flora, however, caution must be used to distinguish carefully two radically different types of endemic plants: those under discussion, which were local in origin and have never spread abroad; as contrasted with those which owe their present localization rather to the fact that they are isolated survivors of genera or species at one time much more widely distributed. The former category, which we may call the "indigenous" endemics, will evidently represent a new element in the flora; the latter, or "relict" endemics, a very old one. It is not always easy to separate sharply these two types in a given flora, but species, and especially genera, which stand apart and possess no near relatives in the region are, in most cases, at least, evidently to be looked upon as relicts; whereas in a group of species or genera the members of which are numerous and closely related one to another we doubtless behold a body of plants undergoing evolutionary development on the spot.

It is an analysis only of the latter type which is of significance for the present problem.

The genera of dicotyledons endemic[1] in temperate North America (Canada, the United States and northern Mexico) and in Europe (inclusive of the entire Mediterranean floral province) were studied in this connection. 400 genera were recorded as being endemic or essentially so in temperate North America. In this imposing array of types which are limited in their distribution to this region approximately 130 stand in isolated positions in the flora, being quite without near relatives, and are presumably "relicts." To this category belong *Carya, Planera, Maclura, Garrya, Sassafras, Xanthorrhiza, Baptisia, Nemopanthus, Ceanothus, Dirca, Dionaea, Hudsonia, Rhexia, Ptelea, Decodon, Houstonia, Symphoricarpos* and many other familiar plants. That these now exclusively American genera were indeed at one time much more widely distributed is indicated by the fact that many of them are found as fossils in Europe and Asia to-day. They undoubtedly represent a very ancient element in the flora. The most noteworthy feature of these "relicts" is that they include practically all the genera of *woody* plants endemic to this region, the typically American trees and shrubs.

Such ancient and isolated relicts, however, compose but a minority of the endemic genera. The remainder evidently belong to the other category and owe their endemism rather to the fact that they have been developed in America and have never spread beyond its borders. It is such endemic types which are of interest to our problem. That they are actually of local origin is rendered probable by their occurrence in groups of closely related genera (many of which are rich in species) each group presumably representing a separate center of evolutionary development and the nucleus for a new subfamily. There

[1] Genera in which 90 per cent. of the species or more are confined to the region in question were considered as endemic there. Genera rather than species were studied since they represent a greater degree of evolutionary change; and since endemism among species is so nearly universal on the two continents as to make its investigation of little value.

are over sixty such groups of allied genera in the endemic flora of North America. Notable among these are the alliances centering about *Eriogonum* in the Polygonaceæ; about *Streptanthus* and about *Lesquerella* in the Cruciferæ; about *Eschscholtzia* in the Papaveraceæ; about *Heuchera* in the Saxifragaceæ; about *Cercocarpus* in the Rosaceæ; about *Godetia* in the Onagraceæ; about *Cymopterus* in the Umbelliferæ; about *Pterospora* in the Pirolaceæ; about *Cryptanthe* in the Boraginaceæ; about *Trichostema* and about *Agastache* in the Labiatæ; about *Pentastemon* and about *Castilleja* in the Scrophulariaceæ, and about *Brickellia,* about *Solidago,* about *Boltonia,* about *Silphium,* about *Rudbeckia,* about *Hemizonia,* about *Baeria,* and about *Microseris* in the Compositæ. Most of these groups of genera have their center of distribution in the southwestern United States or in northern Mexico. The great majority of endemic genera in Europe are also evidently "indigenous" rather than "relict" in character. Centering chiefly in the Mediterranean region there are seventy or more groups of closely allied genera, notable among which are the alliances dominated by *Dianthus, Brassica, Alyssum, Lotus, Scandix, Asperula, Scabiosa, Anchusa, Anthemis, Carduus,* and *Cichorium.*

These "indigenous" endemic genera constitute a very characteristic and important part of the present-day flora of North America and Europe. Had they existed in anything like their present numbers and importance at the period when an easy exchange of plants was possible between the two northern continents, it is hard to believe that they would not now be well represented in the floras of both; particularly since herbs, of which we shall see these genera to be almost exclusively composed, tend more quickly than any other plant type to loose their endemic character because of the power to migrate rapidly and populate wide areas which is conferred by their ability to produce seed from seed in a single generation. This is well shown by the fact that in DeCandolle's famous list of 117 species, each of which at present occupies at least one half of the land area of the globe, there are none but her-

baceous forms. Since we have cause to believe that communication between North America and Europe existed until well into the Tertiary, the supposition is altogether reasonable that the genera in question have undergone at least the greater part of their development and dispersal since that time; and that in contrast to the "relicts" and the non-endemic genera they represent an element of very recent development in the floras of the two regions.

It is noteworthy that these indigenous endemic genera are composed almost exclusively of herbaceous species, *Cercocarpus* and its allies among the Rosaceæ furnishing practically the only exception to the rule in America. If the conclusion is correct that such endemic types are the most recently developed members of a flora, this dominance of the herb among them constitutes excellent evidence that it is the herbaceous element which has indeed been undergoing the most rapid evolutionary change.

In striking contrast to the highly endemic and local character of so many of the north temperate genera of herbs is the wide geographical range almost universal among the woody types. Nearly all the tree genera of temperate North America exist to-day on some portion of the Eurasian continent or give evidence by fossils that they once did exist there. The whole study of endemism in its relation to growth forms presents us with the picture of a very slowly changing woody vegetation, one which since the separation of the two northern land masses has given rise to few or no generic types, but which has been accompanied by a rapidly developing herbaceous flora so quick to originate new forms that upon isolation it has produced not only a throng of local species, but even a goodly number of genera.[2]

Evidence of value in the present problem may also be derived from a study of the relationship of the members

[2] The predominance of woody plants which is so pronounced in the endemic element of the floras of oceanic islands and of somewhat isolated continental areas in the south temperate zone, is evidently due to the fact that most of the herbaceous portion of the vegetation here has so recently arrived from its seat of origin in the great land areas of the north, that it has not yet had time to develop into endemic species and genera on a large scale.

of the various growth forms and their distribution in the modern system of plant classification. During the history of the vegetable kingdom, the continual evolution of species, genera and families has been opposed by their continual extinction, for one cause or another. One would expect that those types in which evolution was proceeding most rapidly would occur in groups, usually rather large, of closely related species and genera, and that members of such groups which subsequently came to be isolated by the extinction of their allies would soon become centers of development and give rise again to new groups. Monotypes would consequently be rare among them. The more slowly evolving forms, on the other hand, would be able to repair the ravages of extinction much less rapidly and easily and would therefore tend to occupy more or less isolated positions in the system, frequently as monotypic genera or families.

To determine the distribution of herbs as contrasted with woody plants in the present scheme of classification an analysis was made of the dicotyledons in Engler and Prantl's "Naturliche Pflanzenfamilien," supplemented and brought up to date as far as possible by the seventh edition of Engler-Gilg's "Syllabus der Pflanzenfamilien." The figures obtained of course can not be regarded as exact, but they are at least definite enough to bring out certain general facts.

One hundred and eight thousand species of dicotyledons were counted, grouped in 6,840 genera and 238 families; 4,030 genera, comprising slightly over 50,000 species, were found to be composed entirely of woody plants, and 2,630 genera, with slightly under 40,000 species, entirely of herbs; 180 genera, containing over 18,000 species, included both woody and herbaceous members and were disregarded in the count.[3] The average number of species in the woody genera is therefore 12.5, in the herbaceous ones, 15. In their large genera (including 10 species or more) the two

[3] If 90 per cent. of the species of a genus were woody, that genus was counted as "woody"; if 90 per cent. were herbaceous, it was counted as "herbaceous." "Mixed" genera include more than 10 per cent. of each type.

types are practically the same, there being an average of 45 species per genus in the former and 46 in the latter. This of course pulls the general averages together. The more scattering distribution of trees and shrubs, however, is made evident by the fact that of small genera (10 species or less) they possess 3,115, as compared with 1,890 for herbs.

The two types are somewhat more diverse in the number of genera per family. In an analysis to determine this distribution, only land plants of normal growth-habit were considered. The Balanophoraceæ, Rafflesiaceæ, Hydnoraceæ, Lennoaceæ and Cynomoriaceæ were excluded as aberrant; and families characteristically aquatic were also omitted, since from their uniformity of environment or other reasons unknown they are notoriously poor in generic types. Two hundred and twenty-four families of dicotyledons enumerated in the seventh edition of Engler's "Syllabus" remain to be considered; 130 of these are exclusively woody, 60 have both woody and herbaceous members, and only 34 are exclusively herbaceous,[4] making it evident at a glance that woody plants have much the wider taxonomic distribution. In the 190 families which include trees and shrubs, there are just 4,000 genera, an average of 21 per family. In the 94 families which include herbs, there are 2,590 genera, an average of 27.5 per family. (The 180 "mixed" genera were left out in this count.) The fact that the bulk of genera in both are massed in a few large families again pulls the averages together; but the more scattering distribution of woody genera over a large number of small families is decidedly emphasized when we note that there are no less than 39 monogeneric families of trees and shrubs, but only 7 of herbs (exclusive of aquatics). Of families with 5 genera or less there are among woody plants 83, among herbs only 24. In number of species per family the differ-

[4] Families like the Ranunculaceæ, Papaveraceæ, Crassulaceæ, Geraniaceæ and Umbelliferæ, which possess exceedingly few woody species, have been counted as strictly herbaceous; and others like the Sapindaceæ, Araliaceæ and Bignoniaceæ, in which there are very few herbs indeed, have been counted as strictly woody.

ence between the two types is still more marked, for the 190 woody families include about 59,000 species, an average of 310; the 94 herbaceous families about 49,000 species, an average of 510.

It is therefore evident that herbs tend to be massed in a comparatively few large genera and families. Among trees and shrubs, on the other hand, although the majority of species are also naturally in large, successful groups, there is a very much greater proportion of small genera and especially of small families, widely scattered throughout the whole taxonomic range, which have been isolated by the wholesale extinction of related forms and are apparently very slow to develop into larger aggregations. Such evidence as this, like that derived from a study of indigenous endemism, seems to indicate that the rate of evolution among herbs is decidedly higher than among woody forms.

There are doubtless numerous exceptions on both sides. *Crataegus, Eucalyptus, Acacia* and other genera of trees and shrubs appear to be rapidly developing new species, whatever the cause thereof may be; and many herbs, far from producing new forms, show every indication of being stationary or even of becoming extinct. These are both evidently exceptions to the general rule, however.

Of course these cases introduce the consideration of another factor, naturally thought of first in connection with rate of evolution among any organisms, namely, their comparative "variability," using the term in its broadest sense. To contrast members of the two growth types as a whole in this respect is necessarily very difficult, but an attempt was made to do so by comparing the proportion of varieties and named forms among the woody plants with that among the herbs in a number of floras. The results are shown in the table (p. 474).[5]

The proportion of varieties and forms is therefore practically the same among woody plants as it is among herbs, and if this is to be regarded as at all a criterion of variability, there is little to choose between the two growth

[5] Dicotyledons only are considered.

	Species		Varieties and Forms	
	Woody	Herbaceous	Woody	Herbaceous
N. E. United States....	532 (23%)	1,748 (77%)	144 (31%)	322 (69%)
Ceylon.....	1,123 (63%)	670 (37%)	165 (60%)	112 (40%)
Australia.....	3,970 (70%)	1,741 (30%)	752 (70%)	325 (30%)

forms. The greater plasticity probably belongs to the herb, owing to the larger independence of environment which its discontinuous existence allows. Brevity of life-cycle, however, rather than higher variability, is probably the cause of the more rapid rate of change exhibited by members of this type.

The conclusion that herbs have been evolved much more rapidly than trees or shrubs has certain important corollaries. There are at present approximately 2,600 genera of dicotyledonous herbs and 4,000 genera of woody plants. The much wider taxonomic range which we have noted in the latter type makes it probable that in extinct species and genera their numerical superiority is still greater. If herbs are thus decidedly fewer than woody plants in number of species and genera, but are nevertheless being produced at a much more rapid rate, it is highly probable that the herbaceous element in the flora of the world must have had a shorter evolutionary history than the woody one. This is in harmony with a considerable body of evidence derived from a study of the history, structure and distribution of the Angiosperms, which indicates that the most ancient members of the group were woody and that herbaceous vegetation has made its appearance in comparatively recent geological time.[6] The great steps in the evolution of the higher plants seem to have taken place while trees and shrubs were the dominant growth types, for all the important orders and the great majority of families are still composed wholly or in part of such plants. Herbs occur to-day in less than half the families of the dicotyledons, and although such a dominant portion of the vegetation in many regions, they seem to be of relatively recent appearance.

[6] Sinnott, E. W., and Bailey, I. W., "The Origin and Dispersal of Herbaceous Angiosperms," *Annals of Botany*, XXVIII, 1914, pp. 547–600.

A study of the comparative rate of evolution among the Angiosperms also throws a little light on the antiquity of this great group. Its fossil representatives have as yet failed to make their appearance in strata lower than the lowest Cretaceous, and it is commonly assumed that they had their origin at about that period. We have already noted the probability that they were represented at their inception only by woody forms. There is evidence that the herbaceous type, save perhaps as a negligible portion of the flora, did not arise till the early Tertiary, since which time its members have undergone practically their entire evolutionary development. As to the relative lengths of geological periods there is no very definite evidence, but authorities agree that the Mesozoic was of considerably longer duration than the Tertiary, a conservative estimate placing the former at about three times the length of the latter. Let us grant for purposes of argument that this is a reasonably close approach to the truth; and let us also assume that herbs have evolved at a rate averaging twice as great as that of woody plants, surely a moderate supposition. All the 2,600 exclusively herbaceous genera presumably developed as herbs; and there are 4,200 genera which contain woody plants and which probably originated as woody plants. Now if these 2,600 herbaceous genera have been developed since the beginning of the Tertiary, woody plants, producing new forms at half this rate, would during the same time have given rise, let us say, to 1,300 genera. To produce the other 2,900 woody genera (to say nothing of the hundreds which have become extinct) would require, assuming the same rate of evolution, another period twice as long as the Tertiary, thus thrusting back the origin of the Angiosperms to a date distant from the present thrice the length of the Tertiary. According to the estimate mentioned above, this would be about the beginning of the Jurassic. Of course this is all extremely hypothetical, but it serves to emphasize the probability that in order to have developed their great number and diversity of slowly changing

woody forms, the Angiosperms must have been in the process of evolution for a period many times as long as that since the origin of herbs, evidently beginning at a date far earlier than that at which the first angiospermous fossils occur.

This conclusion is still further strengthened by other facts. The earliest fossil Angiosperms seem to have been trees, presumably the most slowly alterable type of all. Furthermore, whatever may have been the importance in recent times of hybridization through cross-fertilization by insects as a cause of accelerated evolution, this factor was evidently inoperative at the origin of the Angiosperms, since, according to Handlirsch, flower-loving insects did not make their appearance till the Tertiary. The specialized character and apparently high phylogenetic position of many of the earliest fossil Angiosperms also renders it highly probable that they were the product of a long evolutionary history.

Evidence from all sources therefore seems to agree that the origin of these higher seed plants took place at a time very much earlier than their paleontological record indicates. That they were not preserved as fossils in horizons lower than the Cretaceous is perhaps due to the fact that the earliest Angiosperms, as Professor Bailey and the writer have suggested,[7] appeared under essentially temperate climatic conditions, which in the Mesozoic were mainly confined to upland regions where fossilization would take place much less commonly than in lowlands. This apparent predilection of these primitive Angiosperms for an environment cooler than the tropical, together with what we have noted as to their high antiquity, suggest that the refrigeration of climate which took place in the Jurassic might have been a factor in their origin; and even tempts one to look farther back toward the epoch of markedly low temperatures subsequent to the close of the Paleozoic, which caused so many radical

[7] Sinnott, E. W., and Bailey, I. W., "Foliar Evidence as to the Ancestry and Early Climatic Environment of the Angiosperms," *Amer. Jour. Bot.*, II, 1915, pp. 1–22.

changes in the organic world, as perhaps the time when the angiospermous stock began to be differentiated from its gymnospermous ancestors.

We may point out, in conclusion, that a recognition of differences in the rate of evolution between various growth forms is evidently of importance in many problems concerned with the phylogeny, ecology or distribution of the higher plants. Upon the question, for example, as to whether the boreal species in the floras of southern South America and Australasia are of ancient or recent arrival there, some light is thrown by the fact that these species are almost all herbs. That so many members of a growth-form which is usually subject to rapid change still maintain specific identity with distant northern types argues strongly for their comparatively recent arrival in the south. A similar question is raised by Willis's studies of the flora of Ceylon.[8] He regards the endemic element here as one which is of local and recent origin and as much younger than the non-endemic element; but the fact that of the endemic species, by implication the ones which are changing the fastest, less than one fourth are herbs, whereas nearly one half of the non-endemic species belong to this growth-form, would suggest the opposite conclusion; for had this large body of herbs been in existence here for a very long period, as Willis supposes, we should have expected it to develop a relatively much greater body of endemic species. In such questions as this it should be borne in mind that evolution has not been a steady and uniform process among all forms, but that the decided differences between the various growth types in the rapidity with which they tend to accumulate heritable variations introduces a factor which it is always necessary to consider.

Summary

1. The most recently evolved element in the floras of temperate North America and of Europe, as determined

[8] Willis, J. C., "The Endemic Flora of Ceylon, with reference to Geographical Distribution and Evolution in General," *Phil. Trans., B*, CCVI, 1915, p. 307.

by a study of the indigenous endemic genera, is composed almost entirely of plants which are herbaceous in habit.

2. Herbs tend to be grouped in fewer and larger genera and families than woody plants.

3. It is therefore concluded that herbaceous plants, presumably because of the brevity of their life cycle and the rapid multiplication of generations consequent thereto, are in most cases undergoing evolutionary development much more rapidly than are trees and shrubs.

4. From this conclusion are drawn inferences as to the origin of the herbaceous habit and the antiquity of the Angiosperms.

EGG PRODUCTION AND SELECTION

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ABOUT three years ago breeding for increased egg production was begun at this station with Rhode Island Reds. A report on some of the chief features of the work will be published in the near future, but because of the recent discussion in this journal, by Pearl and Castle, of egg production in relation to selection certain features of egg production in this breed are of particular interest at this time.

The winter record of a hen depends upon two main internal factors aside from possible environmental factors. First, the date at which the first egg of a pullet is produced, which may be taken as an index of the attainment of sexual maturity; and second, the rate of production after the onset of egg-laying. The former in turn depends upon the time when she was hatched and upon her rate of growth. The latter factor, *i. e.*, rate, is controlled in part at least by an internal mechanism. In the Reds it is clear that of the two factors the preponderant effect is exercised by the factor of maturity. The observed differences in rate of production are of less, though by no means negligible importance. In the Barred Rocks, as far as I have been able to learn, conditions are reversed, in that the rate of production appears to exercise a greater influence on the kind of record a hen makes than the age at which she produces her first egg, although the latter is also a factor. Identical records as expressed in number of eggs per unit of time may therefore result, but it is clear that they are not directly comparable. The use of the age at first egg as a criterion of sexual maturity involves some difficulties, but it is the best objective criterion readily available and corresponds at least roughly with the general

bodily conditions familiar to poultrymen as indications of the attainment of maturity. These conditions may be observed in the male as well as in the female. There is also an apparent tendency on the average for large pullets to make lower records than their smaller sisters, as shown by the negative correlation between high winter egg production and large size, due probably to a longer growth period in the larger pullets.

The relation between age at first egg and rate involves the following points: A pullet that matures late can not give expression to high fecundity, although she may carry the genes for it, but the record of a pullet that matures fairly early will depend upon the rate at which she lays. On the other hand, a zero producer will be also late maturing, judged according to the criterion suggested, because she does not lay until spring, provided, of course, that she was hatched at the proper season. It is obvious of course that a high record bird must mature early in order to make her record, and that in this sense early maturity and high productiveness will go hand in hand, but early maturity of itself does not insure a high record, for early maturing birds may lay poorly and so make a low record. On the other hand, late maturity is bound to insure a relatively low record. In the flock of Reds with which we have had to do there is *comparatively* little difference in the rate of production. In one flock the coefficient of correlation for the time elapsing between the first egg and the 1st of March and the number of eggs laid was calculated and found to have a value of $.8612 \pm .0132$ which must mean that the flock was fairly homogeneous in respect to rate of production. In other flocks there is clearly a negative correlation between age at first egg and winter egg production but the values have not yet been determined. The difference between a pullet that begins to lay December 1 and lays 60 eggs, another the first of January and lays 40 eggs, another that begins the first of February and lays 20 eggs, must be a question of start. The last bird, too, must be essentially different from a

bird that begins to lay in November and lays 2 eggs that month, 10 in December, 0 in January and 8 in February, although she lays the same number of eggs as the individual that began February 1. The former is clearly a mediocre producer, the latter a high producer of late maturity.

The flock averages for the past winter, arranged according to the month in which the birds were hatched, are instructive on this point. The mean egg production for the (140) March-hatched birds was 39.8 eggs, for the (172) April-hatched 29.81, and for the (158) May-hatched 18.1 eggs. If the pullets be grouped according to Pearl's classification of zero, 1 to 30 (mediocre), and over 30 (high), there were among March-hatched pullets 6.4 per cent. zeros, 30.0 per cent. mediocre, and 63.6 per cent. high; among the April pullets 11.6 zeros, 37.3 per cent. mediocre and 51.1 per cent. high; while among the May-hatched pullets there were 19.9 per cent. zeros, 58.8 per cent. mediocre and only 21.3 per cent. high. The average winter production for the mediocre and high producers respectively, is for March-hatched birds 17.2 and 54.6; for April 16.6 and 46.2; for May 16.1 and 40.7. In this connection it should be recalled that there is a tendency for the abstract numbers involved to yield similar averages, which are an indication to some extent at least of two genotypes rather than one. Clearly, the time of year during which a Rhode Island Red pullet is hatched plays an important part in determining the class in which a given individual falls.

In general the use of a hen's record expressed in number of eggs per unit of time as the sole criterion of her capacity for egg production seems to us to be essentially wrong. Attention should also be directed to the elements that enter into the make-up of the record. The factor of maturity is not wholly a fecundity factor, though it is closely bound up with egg production and may modify a pullet's fecundity record very considerably. Broodiness is another factor that, although closely associated with

egg production, is after all rather of the nature of a separate entity which may or may not be present, but which when present operates to reduce the egg record of a hen very materially. On the average, a hen's record for the broody months is only about 60 per cent. of the same hen's record for the non-broody months. There is always a sharp break in monthly egg production with the onset of the first broody period and as a hen once broody continues as a rule to alternate brief periods of production with broody periods, it follows that the number of eggs laid depends in a large measure upon the number of broody periods.

Our viewpoint in regard to modifying factors for egg production may be observed in morphological as well as physiological characters. Thus, the color, arrangement and length of hair could not be studied in a hairless race, although the genes for color, arrangement and length may actually exist in the germ plasm of the hairless individuals. Variability in part at least is due to the existence of numerous germinal factors which can come to somatic expression only when some other germinal factor is present. Thus, there are several types of rose comb which appear to be due to definite factors that affect only the rose comb. The spike, for example, may be telescoped into the body of the comb. The telescoped condition is clearly inherited but it does not appear in singles of the same family, although there is no obvious reason why the blade should not be telescoped quite as readily as the spike. Before the rose comb can be said to be understood, the various genetic modifying factors involved, their relations to each other, and the mode of inheritance of each must be made out. Any study of selection that fails to take into account such internal modifying factors is incomplete.

There is no question regarding the inheritance of egg production in the sense that certain families make much better records than some other families, though in the Rhode Island Reds the families that make the better

records also mature at an earlier average age than those making poor records. Whether or not the mode of inheritance of fecundity in Rhode Island Reds follows Pearl's theory is still uncertain. Since there is great variability in the age at which the first egg is produced and since its frequency polygon indicates, at least up to 305 days, the essential homogeneity of the flock, we are inclined to believe that the Reds are unfavorable material for a solution of this question. More work, however, remains to be done before this point can be cleared up.

On Pearl's theory the continued selection of genetic high producers and the continued use of their sons as breeders should in the long run tend toward an improved egg production, even though individual pedigrees are not kept, as he himself has pointed out.

The rate at which the selection becomes effective depends much on what classes are assumed to be available at the start. In the following discussion it is assumed that the matings are made on a scale sufficiently large to permit the various matings to take place in the proportions indicated. The scale required, however, is so large that it would be scarcely practicable to test the matter experimentally.

In the first place, it should be pointed out that of the nine genetic classes of males possible on Pearl's theory, classes 5, 6 and 9 are not produced by any mating of class 1 and 2 females—the only classes laying 30 or more eggs —with any class of males. Moreover, it can be shown that if these three classes be assumed to be the only males available and that if only class 1 females ($l_1 L_1$, $L_2 l_2$) be bred throughout the test and if the male offspring be bred in each generation in the same proportion in which they were thrown by the preceding generation, at about the seventh generation there would be male classes 1, 3 and 7 only, existing in the proportion of 1:2:1. Classes 2, 4 and 8 would indeed be present, but the three classes together would amount to only a little over 1 per cent. of the population. This small percentage decreases one half

in each succeeding generation. The females produced by this group of males mated to class 1 females only, would occur in the proportion of "over 30" females 75 per cent., "under" 25 per cent. The ratio 1:2:1 among the males maintains itself after once reached, so long as class 1 females only are used for mates.

The same ratio is reached if it be assumed that all nine classes of males exist in equal numbers at the start and that they are bred in each generation in the proportions thrown by the preceding generation and only to class 1 females.

The assumptions made have been chosen as those most likely to lead to decreased egg production or to a maintenance of production on a level. I have not worked out many of the possible assumptions, but as long as only females belonging to classes 1 or 2 are used in the matings, males of higher classes, *i. e.*, classes 1, 2, etc., are thrown by those of the lower classes in the same manner as pointed out for classes 5, 6 and 9, so that eventually males of the higher classes come to exist in definite ratios.

If class 2 females ($L_1 L_1 L_2 l_2$) only are bred, somewhat different results are secured. If males belonging to classes 1, 2, 3, 4, 7 and 8 are used in equal proportions at the start (classes 5, 6, 9 being omitted for reasons stated above) then in the seventh generation nearly 98 per cent. of the males will belong to class 1, the other 2 per cent. belong to classes 2 and 3, and these will diminish one half in each succeeding generation. The final result, then, should be a race of high producers.

Since it has been shown that when class 1 females are used exclusively in the matings, that eventually a stable flock of birds is produced in which male classes 1, 3 and 7 exist in a definite ratio, and since if class 2 females are bred exclusively a flock consisting solely of high producers will result in time, and since class 1 females mated to males of classes 1, 3 and 7 throw 25 per cent. class 2 females, 50 per cent. class 1 females and 25 per cent. mediocre producers, it would seem inevitable that eventu-

ally a homozygous race of high producers should result from the continued breeding of the sons of high producers to high producers.

Since Pearl has repeatedly stated that his results apply to annual production as well as winter production, it might be supposed that selection during the Gowell régime should have been effective. Pearl has interpreted the results as due to Gowell's failure to use the progeny test. Two other possibilities, however, suggest themselves. Under the Gowell régime the males came from 200-egg hens, but all hens laying over 150 eggs were used as breeders. Possibly the latter value is too low. The annual production corresponding to the 30-egg division-point for winter production has not been stated, as far as I know, but since the mean annual value of a flock of high producers is stated by Pearl to be about 166 eggs, 150 eggs would seem sufficiently high to exclude mediocre producers. The possibility, then, that this value is too low may be disregarded.

The second possibility relates to the number of males used. In an actual experiment only a relatively few males are used each year. The scale at which the Gowell experiments were carried on was hardly sufficient to equal more than one or two years' work on the scale that would be required to get the males in something like the proportions expected, and hence little or no change in egg production could be expected in the period during which the mass selection experiments were carried on.

While, theoretically, mass selection should be effective under the conditions stated, it would require large numbers in order to be uniformly successful. The progeny test, on the other hand, produces results quickly and definitely.

SHORTER ARTICLES AND DISCUSSION

ON SELECTIVE PARTIAL STERILITY AS AN EXPLANATION OF THE BEHAVIOR OF THE DOUBLE-THROWING STOCK AND THE PETUNIA

My attention has only just been drawn to the paper by Howard B. Frost[1] which appeared in the issue of the American Naturalist for October, 1915, under the title of "The Inheritance of Doubleness in *Matthiola* and *Petunia*." In this paper, which is a preliminary communication, the writer states that from a consideration of the data contained in the accounts which I have published of my experiments on the cross-breeding of pure single and double-throwing strains of stocks (*Matthiola*), he has been led to form a view differing from that which I have put forward as to the interpretation to be placed upon these results. Accepting the essential points requiring explanation to be as I have stated them, he discusses the scheme which I have suggested as underlying and accounting for the facts observed, and also the explanation of these facts proposed by Goldschmidt.[2] Though conceding that the factorial scheme which I have formulated[3] would give the results observed, he rejects it on the ground that it is unnecessarily complex, and claims that his own interpretation, which he then gives, is both simpler and supported by definite evidence. Though it is evident that a final decision on the points raised must await further investigation, we can in the meantime examine in the light of our present knowledge the two main grounds upon which Frost claims that his explanation is to be preferred, viz., (1) its greater simplicity and (2) the existence of definite evidence in its favor.

For the purposes of this comparison we need take into account only the three following outstanding facts:

1. That whereas some single stocks yield *only* singles in each successive generation other strains yield a *mixture* of singles and

[1] As Mr. Frost mentions in a note to his paper that he has received no answer to a letter addressed to me in May, 1914, I may take this opportunity to say that no letter or paper from him has ever reached me, and I can only suppose that his letter in some way unfortunately miscarried.

[2] *Zeitschrift f. induktive Abstammungs- u. Vererbungs-lehre*, Bd. 10, p. 74, 1913.

[3] *J. of Genetics*, Vol. 1, No. 4, 1911, and later *J. Roy. Hort. Soc.*, Vol. XL, Part III, 1915.

doubles in each generation. So far as we know the pure-breeding type and the ever-sporting (double-throwing) type differ in no other respect than this particular character. One can obtain parallel strains of the same color, the same habit, the same form of surface character, the one pure-breeding, the other double-throwing.

2. That double-throwing singles give a small but constant excess of doubles, which we have no reason to doubt is due to a constant excess production among the functional gametes of those carrying the double character.[4] Were this excess merely accidental we should expect to obtain deviations from equality in the direction of deficiency as well as of excess, but such deviations have not been found to occur. The excess of doubles suggests a ratio of 9D : 7S (56¼ per cent. of doubles) or possibly 8·5D : 7·5S (53⅛ per cent. of doubles).

3. That the results of cross-breeding are such as to show that in the pure-breeding single all the functional egg cells and male germs carry singleness, whereas in the double-throwing strain all the male germs and rather more than half the egg cells carry doubleness, somewhat less than half the egg cells and none of the male germs carry singleness. For if the cross is made in the form no-d single ♀ × d-single ♂ all the F_1 singles give a mixture of singles and doubles in F_2, whereas in the reciprocal cross only a proportion—generally rather more than half—of the F_1 cross-breds behave in this way, the remainder give only singles in F_2.

To explain the above facts I have suggested:

1. That singleness is due to the presence of two factors (X and Y).
2. That in the present-day true-breeding single these two factors

[4] That is to say this excess is not apparently due to any selective mortality after fertilization or germination. In previous accounts I have not introduced into my statements the qualifying expression "functional" but I do not gather that any misapprehension has arisen in consequence, since I have clearly shown that my scheme was based on the results ensuing from fertilization—results, that is to say, arising from the nature of those germ cells which did actually function. Until there was any evidence forthcoming of the formation of non-functional germ cells it seemed more misleading to introduce the word than to leave it out. As, however, Frost bases his view entirely on the supposition that some of the germ cells are constitutionally incapable of functioning it becomes advisable for the sake of clearness to express this limitation, previously inferred but not stated, without, however, prejudging thereby the question of the production of non-functional gametes.

occur linked together ($\widehat{XY}$), *i. e.*, they exhibit the kind of relation which is now generally assumed as the interpretation of a widespread class of phenomena.

3. That in the ever-sporting single this coupling or linkage is only partial so that X and Y can occur dissociated.
4. That in this type of single these two factors are distributed differently to the functional male and female germ cells. The male germ cells are unable to carry either factor. The female germ cells may contain both, or one or other, or neither, the four different combinations occurring in the ratio 7:1:1:7 or possibly 15:1:1:15.

These suppositions provide us with a working hypothesis which covers the facts detailed above and enables us to form a conception of how it comes about that the two classes of singles behave as they do.

If 1 and 2 are true, and they postulate nothing beyond what is held to be the probable explanation in the case of other characters studied by other observers, we must suppose that 3 is also. Since were this not so, the offspring of an ever-sporting single having X and Y linked together in any of its functional germ cells, would some of them behave like F_1 cross-breds from the cross no-d single ♀ × d-single ♂ and would yield only a small proportion of doubles, whereas observation has shown that *all* the offspring of ever-sporting singles give an excess of doubles like the ever-sporting parents. Finally as to 4, the supposition of a sex-limited distribution of factors finds also a parallel in other cases: the special features in the present instance are that a sex-limited distribution of factors should occur in an hermaphrodite organism, and that on the male side it should be complete.

So much for the main points of my scheme which are acknowledged by Frost and clearly set forth by him. I now turn to his criticisms.

1. His first point is that I give no reason *why* singleness rather than doubleness is eliminated on the male side, or why this elimination is *uniform*. This is true. But do we know the reason "why" in any case where factors are lost or where they show a sex-limited inheritance? Take, for example, such a case as the red-flowered stock in illustration of the first point. We know that the original wild form was purple-flowered, and we suppose that at some point a mutant arose from which a certain factor B capable of turning a red color blue, much as an alkali turns red

litmus blue, which was present in the wild form, was eliminated. But we do not know *why* the factor B happened to be eliminated rather than either of the other two factors C and R which we suppose to produce red-colored sap, and to be present in the wild form as well as the factor B. We none the less regard the conception of the existence of the factors B, C and R as satisfactorily expressing the color relations in the stock so far as we know them. Neither are we able to say *why* at some point in the course of evolution a mutant arose, which, although inheriting the factors (or factor) governing singleness, produced some functional germs in which these factors were absent. With regard to his further point, viz., that I offer no explanation of the fact that this elimination is uniform (by which I understand him to mean complete) on the male side in the double-throwing single, seeing that it is partial only on the female side, I may point out that neither does he. Indeed it appears to me to be more difficult to explain the facts regarding the egg cells on his view (see below) than to reconcile the production of a uniform type of male germ with mine. So far indeed as the female germs are concerned he does not attempt to formulate any definite scheme. As it is upon their behavior that the observed excess of double offspring depends, one is constrained to ask why the criticism which he passes on Goldschmidt's scheme, viz., that it "gives at most only an indefinite implied explanation of the deviation of the double-single ratio from equality in the double-throwing races," does not equally apply to his own hypothesis. Stated briefly and apart from certain alternative suggestions put forward tentatively in the absence of any positive evidence, Frost's theory appears to amount to this: that single-carrying as well as double-carrying pollen is formed by the ever-sporting single, but that *all* the single-carrying grains contain some other factor which in some way prevents them from functioning. He finds it further necessary to suppose that a similar lethal process occurs in some of the ovules, but that for some (unexplained) reason *some only* of the single-carrying egg cells are rendered functionless, the others are always capable of fertilization.[5] With regard to his question why it is singleness which is eliminated on the male side and not doubleness, it seems unnecessary to point out that as the double-throwing single has arisen from a pure-breeding single,

[5] I conclude that Frost would accept this as a general statement of his position, but he makes no explicit statement regarding the ovules.

if the mutation is one of loss the character lost must be singleness.

But a more important line of argument is that dealing with the question as to *when* the elimination of singleness takes place. At what stage in the sequence of cell divisions occurring in the direct line between the fertilization of the egg cell at the beginning of the cycle and the formation of the male sperm by the factors, and is the disappearance of the single character from the male germs illusory? In other words, is it the case that both single- and double-carrying pollen grains are formed, but that those carrying singleness always fail to achieve their purpose—fertilization? This brings us to a consideration of the question whether, if elimination occurs, it takes place at some point in the series of cell-divisions which culminate in the formation of the pollen mother cells, or at the reduction division, or at one of the succeeding divisions which give rise successively to the complete sporetetrad, the vegetative and generative cells of the pollen grain, and the twin sperms formed from the generative cell. The first alternative Frost dismisses on the ground that we have no decisive evidence in support of somatic segregation and "an overwhelming convergence of probabilities against it." That we have as yet no actual evidence of such segregation in stocks themselves is true but in the light of known facts in regard to bud variation it seems difficult to escape from the view that somatic segregation not only might, but does sometimes occur, and that this possibility is not excluded in the present case.

It appears to be rather generally assumed, though perhaps without sufficient reason, that the segregation of all allelomorphs must necessarily occur simultaneously. Those who hold that the evidence justifies the belief that segregation takes place at the reduction division are naturally committed to the view of simultaneous separation of all allelomorphs. But it must be acknowledged for the reasons given above that there is a certain difficulty in the way of accepting the view that the reduction division of the germ cells constitutes the sole sorting mechanism for the allelomorphs. May it not be, even if the majority of the allelomorphs segregate as a rule at some particular point, that occasionally or even regularly, segregation of one or another pair of allelomorphs may occur prematurely or again may be postponed? All that we certainly know is that by the time the gametes are formed the sorting has been completed. As regards the possibility of elimination at a later stage than the formation

of the pollen mother cells Frost states that, although he has looked for indications suggestive of degeneration among the spor tetrads, he has seen no signs of it at any stage. I may say that the appearance of the pollen in ever-sporting as in true-breeding singles is that it is all consistently good, whereas, any supposition attributing the behavior of the ever-sporting single to degeneration in the grains must needs assume that about half of them are consistently bad. In the absence of any histological evidence in support of elimination of factors *through degeneration of the pollen grains themselves* Frost does not advance it. Adopting the view (as I gather) that segregation must occur at the reduction division, he does not either consider the possibility of elimination at a later point, though the removal from the cell genealogical tree of one daughter cell in each of two successive divisions of the pollen grain leading to the formation of the twin sperms affords precisely the kind of evidence of which he is in search. There remains the alternative view which Frost puts forward, viz., that both single-carrying and double-carrying pollen is produced, but the single-carrying grains never achieve fertilization. In order to get over the difficulty that the male germs of the true-breeding single are undoubtedly single-carrying but are yet able to effect fertilization Frost is compelled to make one of the following alternative assumptions—and here we come to the main point in his scheme:

1. That the pure-breeding single being regarded as SS in constitution, the double-throwing single must not only be supposed to have lost one S factor, but the remaining original S factor must have become altered, or a new lethal factor completely linked with it must have been produced in the double-throwing mutant "by which the presence of S becomes incompatible with pollen formation." In other words, the two processes which Frost postulates as leading to the appearance of the double-throwing single, require (1) the loss of one S factor, and (2) either the production of a new factor producing singleness which we may indicate by S_1 or the complete coupling of the original remaining S factor with some new factor. That is to say, he also finds it necessary on either view to suppose the existence of at least two factors, S and S_1 and in the second alternative to assume further that the two are completely linked. It seems difficult to see wherein this scheme shows greater simplicity than the one I suggest, which is that singleness is due

to two factors which are completely linked in the true-breeding single type and dissociated in the double-throwing single.

2. As an alternative hypothesis to the above Frost suggests that the pure-breeding single from which the double-throwing single originated may not have been the same kind of single as those which one meets with to-day, but that it differed from them in one or other of the two ways suggested under 1. But again is this a simpler explanation?

Simplicity, however, though not to be disregarded, is not necessarily the final test. Let us consider Frost's second argument that his view can be supported by definite evidence. Failing to find any positive histological evidence that can be taken as indicating the required process of factor elimination, Frost suggests that the case of the ever-sporting single is to be considered as that of a *hybrid showing selective sterility*. To quote his own words:

> Selective partial sterility seems to be rather a common phenomenon, and it very probably occurs here.

Functional sterility is to be supposed in the case of all pollen grains carrying the factor (or factors) essential to singleness, *i. e.*, according to Frost's scheme, either S_1—a modified form of S, or S with a lethal factor linked to it. In other words, half (we are to presume) of the pollen, though apparently good, is supposed to be incapable of fertilizing the ovules. He further adds that if we also assume "a slight tendency to selective elimination of S-carrying eggs"—a somewhat vague supposition to account for a very definite fact—or if these egg cells were less often fertilized than those which are s in constitution, or if there were selective elimination of the embryos (Ss) that would produce singles, we should have "a simple and direct" explanation of the constant excess of doubles. It is in fact suggested that the postulated inability of the single-carrying pollen to fertilize the ovules may be due to want of vigor. As bearing on this point he calls attention to the greater vigor of the double as compared with the ever-sporting single, as shown in the vegetative habit of the growing plant, and in the greater viability of the double-carrying embryos (seed). This greater vegetative vigor of the ss over the Ss zygote Frost contends may possibly be the outcome of a similar difference between the s and S gametes. But if this were so, if the lesser vigor of the ever-sporting single is due to the presence of *one* S fac-

tor, surely we should expect that the true-breeding single, which is SS in constitution, would be less vigorous still. It seems somewhat gratuitous to suppose that the character singleness is sometimes due to a factor S associated with greater vigor and sometimes to a factor S_1 associated with diminished vigor; or, to put it another way, to assume that if it is the lack of one dose of the factor for singleness in the ever-sporting plant which makes it less vigorous, that the lack of the double dose in the double plant leads to the opposite result of greater vigor. Is it not almost a certainty that the greater vigor of the double-flowering plant is due to the fact that the energy of the individual is not exhausted in the formation of the reproductive cells, but is expended in producing a more vigorous vegetative growth? And hence that a check to vegetative growth, similar in cause and in degree, is operative alike in the pure-breeding and the double-throwing single? To obtain strict proof that this is so is difficult since it might always be argued that the particular pure-breeding single strain used as a control was not precisely identical in all other respects with the double-throwing strain with which it was being compared. It can, however, be stated that in some commercial material supplied as double-throwing, but which proved to be a mixture of pure-breeding and ever-sporting singles otherwise apparently identical, no indication was observed of any difference in vigor between the two kinds of singles. The second argument which Frost urges in support of his hypothesis of differential sterility is the fact that the seeds (embryos) which produce doubles have on the whole rather greater viability than their sister seeds which give singles. But this second argument, depending for point on the same entirely unsupported assumption as that derived from vegetative habit, is open to the same objection. I have never observed that the seed-producing true-breeding singles showed any superiority as regards viability over that yielding the ever-sporting singles, but rather, as with vegetative habit, that the distinction is to be drawn between any kind of single-producing seed on the one hand, and double-producing seed on the other. I have sown a large quantity of apparently excellent seed of a pure-breeding single after the lapse of some years and failed to get any germination, just as I have failed sometimes to get any singles from old double-throwing seed although a few doubles were obtained. Lastly, Frost brings forward the somewhat out-of-date view that the percentage of

doubles is increased by starvation treatment. Though this treatment is still practised by German growers, it survives from a time when it was not yet appreciated that the capacity of the individual to become a single or a double depended upon its inherited constitution and not upon the effects of environment.[6] It may be pointed out that the French growers have been in the habit of pursuing precisely the opposite method of treatment with the same object in view. The inhibition of flowering which Frost has observed to be more marked in the singles than in the doubles in the case of one variety when subjected to a high temperature does not seem to me to bear on the question at issue,[7] which is whether there is any direct evidence of the selective sterility of ovules and pollen in the ever-sporting as compared with the true-breeding single. For I gather that Frost is not prepared to maintain that sterility occurs regularly also in the pure-breeding single as well as in the ever-sporting single. It is further to be noted that besides assuming the definite sterility of all the S_1 pollen in an individual of S_1s constitution presumably producing equal numbers of S_1 and s grains, Frost has to have recourse to the vague assumption that there is only a *slight tendency* to selective elimination of the S_1 *egg cells* out of a total composed presumably of equal numbers of S_1 and s. One is fain to ask on what grounds it is possible to uphold the view that the same factor can destroy the functional activity of every pollen grain carrying it, but is only able to affect some of the egg cells in which it is borne? In this connection it may be mentioned that it is no uncommon circumstance even when self-fertilization is left to nature to obtain pods both in pure-breeding and double-throwing singles where every ovule has been fertilized, and this can always practically be ensured where fertilization by hand is carried out in good weather. Though he instances no examples I gather from his previous reference to Belling's work that he has in view such cases as that of *Stizolobium deeringianum* (the Florida Velvet "bean") and other species investigated by that observer,[8] *Nicotiana* on which recent experiments in this connection have been

[6] The real advantage of the German method of treatment is that the seed harvested is all well ripened.

[7] On this subject of the inhibition of flowering, however, Frost promises further information.

[8] *Zeitschr. f. ind. Abst. u. Vererbungslehre*, Band XII, 1914.

made by East,[9] and *Œnothera* studied by Geerts.[10] But in these cases we are dealing with species hybrids, with plants in which partial sterility is a demonstrable fact and due to a demonstrable cause. In the case of *Nicotiana* the parent plants were both (one certainly, the other in all probability) self-sterile and thus the cause of self-sterility in the cross-bred offspring is explained. In *Stizolobium* Belling found, as Geerts had previously noticed in *Œnothera,* that in the hybrids a certain proportion of both ovules and pollen grains were shriveled and malformed. Here again the cause of the sterility is plain. If, as Frost suggests, the ever-sporting single stock should be regarded as a hybrid, it differs completely from the cases referred to above, for in this case there is no obvious sign or cause of sterility either in the plant itself or in the pure-breeding single from which we suppose it to have arisen. It becomes then a question whether to attach weight to the argument from analogy in a case where it goes against all the evidence available.

From the considerations here reviewed I am led to sum up the position as follows:

Evidence is wholly lacking in the stock itself in support of Frost's hypothesis that the behavior of the ever-sporting (double-throwing) single is to be accounted for as the result of the selective sterility of ovules and pollen. Not only so, but it may be claimed that the facts on which he relies to support his argument can equally well be adduced in favor of the opposite point of view. The selective elimination of embryos or the more frequent fertilization of egg cells of s as compared with those of S (or S_1) constitution seem both untenable in view of the fact that the usual excess of doubles is obtained in cases where every ovule is fertilized and every resulting seed germinates. In the formal scheme which I have put forward we have a working hypothesis which enables us to correlate the present known facts. Does Frost's hypothesis give us more than this? Are we not, in the end, still left debating whether his various speculations unsupported by facts really carry us further, and whether they can justly lay claim to the merit of greater simplicity?

There is, however, one further point of interest bearing on this discussion to which I would call attention here. According to the scheme which I have suggested the constitution and gametogenesis of the two kinds of single can be represented thus:

[9] THE AMERICAN NATURALIST, Vol. XLIX, No. 578, 1915.

[10] *Récueil des Trav. Bot. Neerl.*, Vol. 5, 1909.

Ever-sporting Single XYxy		Pure-breeding Single (as it is Found in Ordinary Commercial Material) $\widehat{XY}\widehat{XY}$	
Gametes		Gametes	
Ovules	Pollen	Ovules	Pollen
7 XY or 15 Xy 1 Xy 1 xY 7 xy or 15 xy	all xy	all $\widehat{XY}$	all $\widehat{XY}$

the presence of X and Y in the zygote always producing singleness, whether the factors are coupled or not.

Now on this supposition the mating d-single ♀ × no-d single ♂ will give some plants of the constitution $\widehat{XY}\widehat{XY}$. These when self-fertilized will presumably give some pure-breeding F_2 plants of XYXY composition. If these pure-breeding singles in which X and Y are not coupled are crossed back with the pollen of an ever-sporting single we shall again have a plant with the constitution XYxy. In this way we may hope perhaps to synthesize the ever-sporting form. This experiment is already in progress. For this purpose the ever-sporting strain known as sulphur-white is particularly well suited if used as the female parent in a mating with a pure-breeding cream. As the ovules of the sulphur-white appear to be of the four kinds, XYW, XyW, xYw, xyw, we know that *only* F_1 single whites will serve our purpose. We also know that we can disregard among the F_2 families derived from the self-fertilization of F_1 whites those which contain doubles, and proceed to cross individuals in the pure-single families with pollen of an ever-sporting type. By the choice of a sulphur-white as the female parent in the first cross we are saved much trouble in identifying those F_1 plants which contain XY unlinked. In this way we may hope to obtain further light on the different condition of the factors for singleness in the pure-breeding and ever-sporting single, respectively.

After dealing with the stock Frost suggests that his hypothesis of selective sterility no doubt also explains the case of *Petunia,* and adds that in any case my view that singleness is here dominant is untenable. He further mentions that both Goldschmidt and Belling[11] hold the view that doubleness and not singleness is

[11] Belling's statement is that "in the *Petunia* doubtless *may* be incompletely dominant as in the greenhouse carnation." THE AMERICAN NATURALIST, Vol. XLIX, No. 578, p. 126, Note 1, 1915.

dominant in this case. In my account[12] of the results obtained with horticultural strains of *Petunia violacea* and *P. nyctaginiflora* and a hybrid double form I suggested that we might account for the following facts:

1. That the singles when self-fertilized or inter-bred gave only singles.
2. That when crossed with the pollen of doubles they gave both singles and doubles in F_1, the singles being in excess though not always in the same ratio.

by supposing either

(*a*) That some factor essential to singleness was absent from all the ovules of the singles and from some of the pollen of the singles, or conversely

(*b*) That some factor was absent from all the pollen of the doubles, but only from some of the ovules of the singles,

(*c*) Also that more than one factor was concerned in determining the single-double character, and

(*d*) That singleness is dominant.

It will be seen that the above suppositions provide only a general basis of explanation; they do not constitute a full solution even of the facts observed. Frost, putting (*c*) on one side on the ground that it concerns only the deviation of the ratio from 50 per cent., argues that both (*a*) and (*b*) are untenable. He regards the facts as indicating that doubleness and not singleness is dominant, and holds the view that if some of the pollen of the doubles be assumed to carry doubleness and some singleness the hypothesis of partial sterility will explain the rest. But though the formulation of (*c*) was intended primarily to provide for the occurrence of more than one ratio, it was essential also to the suppositions (*a*) and (*b*). If (*c*) is negatived then (*a*) undoubtedly becomes impossible, but if (*c*) is true then (*a*) or (*b*) might represent a basic part of the explanation with which some further complication was combined, as to the nature of which, however, the data available afforded no clue. Owing to the complete sterility of the double plant, it was impossible to make the reciprocal cross. The singles employed might be, in fact almost certainly were, of mixed descent. It was realized that at best either scheme offered only a partial solution. Unfortunately the efforts made in the course of the experiments and since, to obtain seeds of the wild species, have only been partially successful. The position

[12] *Journal of Genetics*, Vol. 1, No. 1, 1910.

still is that we are unable to say for certain whether doubles invariably occur when the above-named species are crossed with the pollen of a double. When this evidence is available we may expect it to throw further light on the question as to which character is dominant. At present decisive proof on this point is lacking. Comparison with the other types carries us no further. Singleness has been found to be recessive in carnation, hollyhock and *Meconopsis cambrica;* on the other hand,—it is dominant in wallflower and probably in sweet william.[13] Moreover, these forms differ from *Petunia* in that they give a *uniform* F_1 when single and double are mated together. The case of *Petunia* therefore still remains one of balance of probabilities. In regard to Frost's further suggestion that the facts observed are due to selective sterility I think that this hypothesis may very possibly be correct and certainly has some evidence in its favor. *P. vidacea* is recognized as a self-sterile species and many of the singles which I used proved to be so. A large number of individuals were tested for this character, but further investigation was postponed in the hope of obtaining pure material for comparison. If Frost's hypothesis is confirmed for *Petunia,* and the work of Belling[14] and East[15] points in this direction, it may offer a complete explanation of the facts and render the supposition of a differential distribution of factors to ovules and pollen in this genus unnecessary.

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GAMETOGENESIS IN PLANTS

THE evolutionary origin of the reproductive cells furnishes one of the most fundamental problems connected with genetics, for upon a clear understanding of the subject depends the satisfactory solution of many subsidiary problems relating to animal and plant breeding. The value of hybridization and inbreeding; the meaning of the pure line hypothesis; the principle of cumulability, etc., may here be mentioned. Therefore, whether or not one agrees with the conclusions presented, studies from widely

[13] Saunders (unpublished). The carnation has also been investigated by Norton. (See paper read at the meeting of the Society of Horticulture in Philadelphia in December, 1904. Also *Gard. Chron.*, Jan., 1905.)

[14] *Loc. cit.*

[15] *Loc. cit.*

divergent standpoints which bear upon the question are to be welcomed. It is only through an analysis of the opinions thus advanced that there will develop a perspective which will eventually permit the solution of the problem.

It is in this connection that the conclusions of Professor Coulter as set forth in "The Evolution of Sex in Plants"[1] are of interest, representing as they do the views of one whose attainments in biology have by no means been confined to the field of plant morphology. Presented in a clear and interesting manner so far as the facts are concerned, the volume furnishes a valuable résumé of the subject from the botanical standpoint. It is evident, however, that a certain narrowness must exist in such a presentation, for a problem of this nature demands that plant biology and animal biology supplement one another from the experimental as well as from the morphological and cytological side. Gametogenesis had its beginning not, as Coulter suggests, among organisms far above the most primitive plants, but among unicellular flagellate forms whose representatives partake of the nature of both plants and animals and from which have arisen the various groups of plants in general. Sexuality, once having arisen, may have been partially or even wholly suppressed in various plant groups, but its subsequent reappearance by no means makes it necessary to affirm its polyphyletic origin. Our present knowledge of Mendelian behavior is of interest in connection with such a view.

It will be well to examine some of the more definite conclusions which Coulter has presented. Few of these are original, nevertheless they are of decided value since they are in most cases supported by unique observations bearing directly upon the point of view. It is merely unfortunate that the bibliographic references which would illustrate the development of the ideas are entirely absent, in consequence of which a false impression may be conveyed to many readers.

Early in the volume it is stated that sex in the higher animals has become the only method of reproduction. Logically this view is not to be maintained, as has already been pointed out by LeDantec ('03) as well as by Chamberlain ('05) evidently in ignorance of the conclusions reached by the previous writer. More recently Janet ('12) has considered the subject. If the criterion by which the sporophyte is to be distinguished from the

[1] By John Merle Coulter, head of the department of botany, Univ. of Chicago. Univ. of Chicago Press, December, 1914.

gametophyte rests upon the $2x$ as compared with the x condition of the chromosomes, we find that among animal organisms the asexual phase has actually become the dominant method of reproduction and the sexual phase is represented only by the parasitic cells arising through the reduction division. In accordance with this view one is prepared to accept the spore mother cells of plants as homologues of the cells preceding the reduction division in animals. In a subsequent discussion Coulter states in accordance with the view first advocated that the animal body produces gametes and not spores. When reduction occurs at the time of the first maturation division in animal organisms it is quite clear that the cells thus produced may correspond to spores which in the next division give rise to gametes. It may even be asserted that they are megaspores or microspores dependent on the sex represented. When chromosome reduction is moved forward to the second maturation division, however, it is possible to agree with Coulter, but seemingly more logical to admit that the change is a secondary one and that the first maturation cells may still represent the spore cells.

In accordance with the proposition that spores unite as gametes to form a single cell, evidence should either be presented to show that an identical chromosome composition exists between the actual spores and the so-called spores functioning as gametes or consideration should be given to subsequent reduction division. Otherwise the conclusion scarcely merits the value of an opinion. Furthermore, the argument that the fusion of a sperm and cell among the angiosperms to form a nutritive endosperm justifies the conclusion that pairing and fusing do not represent the essential features of sexuality, can not be considered. This is only one of numerous examples where changes in form or function of parts occur without having any bearing on the actual origin of the part. Even in this case a fusion is represented and may have a value similar to that among gametes.

It is in connection with "A Theory of Sex" that it seems necessary to decidedly differ from Professor Coulter. Here the two main theses are that sexuality has arisen (1) to carry an organism through an unfavorable environment, and (2) to make evolution more rapid by presenting a greater diversity of forms.

The first deduction is based on the proposition that gametes in many plants are produced at the close of the vegetative period. Such a conclusion—*post hoc ergo propter hoc*—does not rest upon a sound basis. With the fulfilment of a function having the

importance of a gamete production, it is quite logical that the cycle of development should close, but to state that the closing of the cycle has brought about the production of the gametes, is quite another thing. The acceptance of this would lead to the inference that gametes arose in fresh or brackish water forms where pronounced seasonal changes took place and not in larger bodies of water like the ocean, the most probable place.

The second deduction is a restatement of a conclusion reached by Weismann ('76) to the effect that amphimixis increases variability with the assumption that variations thus assumed to be produced are inherited in a cumulative manner. The evidence, however, available at present, supports a view directly contrary to this, namely that the gametic condition makes evolution slower by decreasing the diversity of available forms. Mendelian combinations—amphimutations—may occur but the result is a decrease in variability when the parental populations are compared with the F_2 or with a succeeding generation. The amphimutations are transitory and there is no evidence that they present anything actually new in themselves.

Regardless of the opinions here at variance some of which can only be established as sound generalizations through long experimental investigation, the summary of gametogenesis by Professor Coulter will be read with profit and pleasure by those interested in problems of evolution as well as by those particularly concerned with plant morphology and development.

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NOTES AND LITERATURE

LIFE HISTORIES IN THE RED ALGÆ

THE past decade has given us a number of excellent life history studies in the *Rhodophyceæ* which have been of material assistance in clarifying a very difficult field in plant morphology. The more important of these contributions will form the subject of this review.

Yamanouchi[1] in 1906 published an account of the life history of *Polysiphonia violacea* based on cytological investigations of all of its significant phases. He arrived at the following chief conclusions: (1) Carpospores have 40 chromosomes and tetraspores 20, *i. e.*, half of this number. (2) The sexual plants in their vegetative mitoses showed 20 chromosomes and therefore were believed to arise from tetraspores. (3) The asexual or tetrasporic plants showed 40 chromosomes throughout their vegetative history and consequently could be assumed to come from carpospores. (4) The production on the asexual plants of tetraspores is the result of a reduction division since the first mitosis in the tetrasporangium is clearly heterotypic as shown by the characteristic pairing of the 40 chromosomes and the separation of the members of each pair; thus each tetraspore comes to have 20 chromosomes and is prepared to develop a sexual plant. (5) It was therefore clear that the formation of tetraspores determines the end of a sporophytic generation in the manner characteristic of plants. (6) The gamete nuclei of the sperms and carpogonia take the 20 chromosomes of the sexual plants and fertilization gives the zygote nucleus with 40 chromosomes. (7) Descendants from the zygote nucleus enter the carpospores which consequently have 40 chromosomes and on germination would give tetrasporic plants; certain complicated cell fusions during the development of the cystocarp are purely cytoplasmic in character and evidently nutritional in function. (8) "There is thus an alternation of a sexual plant (gametophyte) with a tetrasporic plant (sporophyte) in the life history of *Polysiphonia*, the cystocarp being included as an early part of the sporophytic phase."

Yamanouchi's contribution on *Polysiphonia* has in great meas-

[1] Yamanouchi, S., "The Life History of *Polysiphonia violacea*." *Bot. Gaz.*, XLII, 401–449, 1906.

ure been the inspiration and largely furnished the basis for the comparative studies that shortly followed. Lewis[2] in 1909 presented an investigation of *Griffithsia Bornetiana* which is in essential agreement with the conclusions of Yamanouchi that an alternation of sexual and tetrasporic plants occurs. From the zygote nucleus, containing 14 chromosomes, are derived the nuclei of the carpospores. The tetrasporic plants have 14 chromosomes and were assumed to come from carpospores. The first mitosis in the tetrasporangium is a reduction division so that 7 chromosomes enter the tetraspores and these were believed to produce sexual plants. Lewis, however, held that the sporophyte generation was represented by the sporogenous cells of the cystocarp and considered the tetrasporic plant to be a phase of an homologous alternation of generations even though it was clear that the tetrasporic plant led up to the critical period of chromosome reduction in the tetrasporangium. From a study of *Griffithsia corallina* Kylin[3] questions the accuracy of the details of nuclear structure and mitoses as given by Lewis and also his count of the chromosomes which in *G. corallina* appear to be as high as in *Polysiphonia*. Kylin describes and figures the reduction phenomena in the tetrasporangium of *Griffithsia* in substantial agreement with Yamanouchi and in an earlier paper gives a similar account for *Rhodomela virgata*.[4]

Extremely interesting are the results of experimental cultures made by Lewis[5] through which fruiting plants have been grown from sporelings established in the laboratory on oyster shells that were then favorably placed in the sea. From carpospores of *Polysiphonia violacea* 6 tetrasporic plants were developed and 23 sterile. Tetraspores of *Griffithsia Bornetiana* produced a total of 60 sexual plants (32 male and 28 female) and 15 sterile. Tetraspores of *Dasya elegans* gave 149 sexual plants (143 male and 6 female) and 139 sterile, the apparently large proportion of male plants in the culture of this species probably being due to slower maturing of the females. The sterile plants of these cultures were

[2] Lewis, I. F., "The Life History of *Griffithsia Bornetiana*," *Ann. of Bot.*, XXIII, 639–690, 1909.

[3] Kylin, H., "Die Entwicklungsgeschichte von *Griffithsia corallina* (Lightf.) Ag.," *Zeitsch. f. Bot.*, VIII, 97–123, 1916.

[4] Kylin, H., "Studien über die Entwicklungsgeschichte von *Rhodomela virgata* Kjellm.," *Svensk. Bot. Tidskr.*, VIII, 1914.

[5] Lewis, I. F., "Alternation of Generations in Certain *Florideæ*," *Bot. Gaz.*, LIII, 236–242, 1912.

of course individuals which at the time of the examination had not yet developed fruiting organs. More extended studies of Lewis[6] have established the seasonal habits at Woods Hole, Massachusetts, of the above species of *Polysiphonia, Griffithsia* and *Dasya*. Tetraspores and carpospores were germinated on shells that were fastened to piles and left over winter. In June tetrasporic plants of carposporic origin were abundant, which, releasing their tetraspores in July, produced a crop of sexual plants that matured their carpospores in August or early September. The small plants from the carpospores winter over and produce the tetrasporic plants of the first summer generation. Thus the sexual generation is conspicuous in the late summer while tetrasporic plants surviving the winter are characteristic of the spring. Belated growth of tetrasporic plants may result in their fructification late in summer, so that a few small carposporic plants also winter with the tetrasporic but they are relatively scarce. The seasonal history is then in the main characteristic; tetrasporic plants appear in the spring and through their spores produce a summer crop of sexual plants, from the carpospores of which a generation of small tetrasporic plants in favorable situations carries the species through the winter. This experimental work thus supports at all points the conclusions of Yamanouchi based on cytological studies.

The most important cytological work on life histories in the red algæ since the paper of Yamanouchi on *Polysiphonia* is that of Svedelius presented in studies on *Martensia, Delesseria, Nitophyllum* and *Scinaia*. Part of this work, described in the next paragraph, concerns the development of tetraspores in multinucleate tetrasporangia (*Martensia* and *Nitophyllum*). All of it supports to the fullest degree Yamanouchi's theory of alternation of generations in such species as have tetrasporic plants in their life histories. The work on *Scinaia* presents a most interesting hypothesis for the life histories of such red algæ as do not develop tetraspores.

The life history of *Delesseria sanguinea* is discussed by Svedelius[7] in three papers embodying cytological work of a high

[6] Lewis, I. F., "The Seasonal Life Cycle of Some Red Algæ at Woods Hole," *Science*, XXXIX, 253, 1914.

[7] Svedelius, N., "Ueber den Generationswechsel bei *Delesseria sanguinea*," *Svensk. Bot. Tidskr.*, V, 260–324, 1911. "Ueber die Spermatienbildung bei *Delesseria sanguinea*," *ibid.*, VI, 239–265, 1912. "Ueber die Zystokarpienbildung bei *Delesseria sanguinea*," *ibid.*, VIII, 1–32, 1914.

order. Tetrasporic plants have 40 chromosomes in their nuclei. This number is reduced by the first nuclear division in the tetrasporangium. During synapsis the 40 chromosomes become grouped to form 20 pairs, which become exceptionally clear in the stage of diakinesis. The first or heterotypic mitosis separates the members of the pairs, thereby halving the number and giving after the second mitosis 20 chromosomes to each of the tetraspores. Vegetative mitoses in the male and female plants show uniformly 20 chromosomes and it must be assumed that these sexual plants develop from tetraspores. The chromosomes are organized in the prophases of mitosis directly from a chromatic network and without the interpolation of a spirem stage. The spermatangia are cut off in pairs to the right and left of a mother cell and in each spermatangium a uninucleate sperm is organized (20 chromosomes) which on escaping leaves behind an empty cyst. The young carpogonium is uninucleate but an early division differentiates the female gamete nucleus (20 chromosomes) which remains in the carpogonium, and a trichogyne nucleus that shortly breaks down. The carpogonium terminates a 4-celled carpogonial branch borne by a cell ("tragzelle") from which develops also an auxiliary cell and certain sterile cells. The sterile cells enlarge greatly after the fertilization of the carpogonium and then break down, forming a mass of slime which apparently serves to give space and protection for the development of the gonimoblasts. In some way not clearly understood the zygote nucleus of the fertilized carpogonium enters the auxiliary cell and from this cell as a starting point the gonimoblasts arise as a dense growth of short filaments. The cells of the gonimoblasts contain nuclei derived from that of the zygote and consequently have 40 chromosomes which are passed on to the carpospores developed in rows. From the carpospores must come the tetrasporic plants with their 40 chromosomes. We have therefore in *Delesseria* an antithetic alternation of generations exactly parallel with that of *Polysiphonia*, a diploid phase including the gonimoblasts and the tetrasporic plants alternating with a haploid phase represented by the sexual plants.

Svedelius[8] opened a new vista in cytological studies on the red algæ with his discovery of multinucleate tetraspore mother cells in *Martensia*, one of the *Delesseriaceæ*. The young cell has

[8] Svedelius, N., "Ueber den Bau und die Entwicklung der Florideengattung *Martensia*," *Kungl. Svensk. Vet.-akad. Handl.*, XLIII, No. 7, 1908.

like its neighbors several nuclei which by division increase in number as the cell enlarges until about 50 are present. Then a general nuclear degeneration sets in coincident with an increase in the amount of cytoplasm and only one nucleus in the center of the plasma mass survives to give rise to the 4 nuclei that enter the tetraspores. A similar situation was found by Svedelius[9] in *Nitophyllum punctatum,* a related form of the same family, which is described in greater cytological detail. Typical mitoses in the young tetraspore mother cell give it a dozen or more nuclei all with about 40 chromosomes, the diploid number for the species. Many of the nuclei shortly begin to show signs of degeneration by the disappearance of the chromatin so that only the nucleolus remains to take the stain, and there is also a shrinkage of the nuclear membrane. The degeneration is not simultaneous, a few nuclei increase in size and give indications of preparation for the heterotypic mitosis as shown by clear stages of diakinesis. However only one nucleus carries the history of reduction further and thus becomes the surviving nucleus of the tetraspore mother cell, a nucleus very much larger than the degenerating structures that lie about it in the cytoplasm. At diakinesis pairs of chromosomes are clearly shown, about 20 in number. The members of the pairs are separated by the first mitosis which is therefore heterotypic and a reduction division as in *Polysiphonia, Griffithsia* and *Delesseria.* The second mitosis, homotypic, gives the four nuclei of the tetraspores, each with about 20 chromosomes. It is very interesting to note that the red algæ present illustrations of nuclear degeneration at a period of reproduction when it may be desirable to conserve the cytoplasm of a cell for a limited number of reproductive elements. This nuclear degeneration appears to be strictly analogous from a physiological point of view to that exhibited in the oogonia of *Vaucheria, Saprolegnia* and *Albugo,* in the sporangium of *Derbesia,* and in the oogonia of certain forms of the *Fucaceæ.*

With the cytological and experimental evidence in complete accord and so strongly in favor of the theory of an antithetic alternation of generations in those red algæ which have tetrasporic plants certain observations which at first thought appear to offer exceptions to this theory naturally take on a high degree of importance. The literature records a number of species which

[9] Svedelius, N., "Ueber die Tetradenteilung in den vielkernigen Tetrasporangiumanlage bei *Nitophyllum punctatum,*" *Ber. deut. bot. Gesell.,* XXXII, 48–57, 1914.

have been reported to bear tetrasporangia on sexual plants. facts which would be significant if it were established that such tetrasporangia were the seat of reduction divisions. Three of these species have been studied cytologically and there is good evidence that the reduction divisions are not present and that tetraspores are either not fully matured or that the "tetrasporangium" develops a monospore. Yamanouchi and Lewis in their studies found occasional sexual plants bearing what seemed to be tetrasporangia but in these cells the nucleus remained undivided in *Polysiphonia* or produced several nuclei in *Griffithsia* while cleavage furrows proceeded only a short distance into the cytoplasm. Svedelius[10] has reported on a cystocarpic plant of *Nitophyllum punctatum* bearing tetrasporangium-like structures. These cells were found around points in the thallus where procarps had been formed and only reached their fullest development when the procarps remained unfertilized. Their position on the thallus therefore indicated a close correlation with the nutritional physiology of the plant. These cells in their early history follow exactly the course of normal tetrasporangia in this species; there is a multiplication of nuclei and then a degeneration of all but one which takes its position in the center of the cell. The surviving nucleus does not divide but the entire protoplast slips out of the thallus as a uninucleate monospore. Since the cystocarpic plant was haploid a reduction division in this tetrasporangium-like cell would have been most irregular; it does not take place and the monospore in its chromosome count has the same value as a tetraspore. *Agardhiella* (*Rhabdonia*) *tenera* presents another problem brought forward by observations of Osterhout. Tetraspores of this plant sometimes germinate while still imbedded in the tissues of the parent with the further peculiarity that the tetrad group behaves as a unit so that all four cells enter into the formation of a sporeling. These epiphytic sporelings commonly become sexual plants, as would be expected from the germination of tetraspores. Osterhout, however, reports that occasional tetrasporic plants are developed which would be irregular unless it were found that such plants came from tetrasporangia in which reduction divisions had been suppressed so that such tetrasporangia, behaving like monospores, give rise to diploid plants (tetrasporic) similar to the generations on which

[10] Svedelius, N., "Ueber Sporen an Geschlechtspflanzen von *Nitophyllum punctatum;* ein Beitrag zur Frage des Generationswechsels der Florideen," *Ber. deut. bot. Gesell.*, XXXII, 106–116, 1914.

they were borne. It is probable that other red algæ will exhibit peculiarities of life history related to apospory, as seems probable in this case of *Agardhiella*.

There is enough evidence before us in these three studies by Yamanouchi, Lewis and Svedelius to demand the utmost caution in the consideration of other cases of "tetraspores" upon sexual plants which have been brought forward by critics of the theory of alternation of generations as applied to the red algæ, cases which have not as yet been subjected to the tests of cytological research. One of the most interesting of these is *Platoma Bairdii* (Farl.) Kuckuck[11] which in Helgoland apparently produces no antheridia but develops cystocarps parthenogenetically. On these cystocarpic plants are also found tetraspores indicating that the plants are diploid in character which if true would account for their apogamous behavior. *Platoma Bairdii* therefore appears to be one of the cases in which sexual organs are developed upon a diploid plant and not one in which tetraspores are found on a haploid generation. A cytological study of this form would be a matter of great interest and the only way in which the facts may be determined. Also, there are the problems of the paraspores or polyspores characteristic of a number of species in the *Ceramiaceæ*. These are spores borne numerously in chains (seirospores) or in dense glomerules and are found on tetrasporic plants. Schiller[12] regards them as homologous with tetraspores, and as supporting the view of Oltmanns that the latter are reproductive spores without significance for an alternation of generations, but until we know the cytology of their development an opinion can have little value. Should the paraspores be formed without reduction divisions, as seems probable, they will rank in the same class with monospores and play no part in an alternation of generations. Should there be found evidence of a heterotypic mitosis in the development of these exceptional reproductive cells they might perhaps constitute a modification of the tetrad group characteristic of reduction divisions, but it does not seem likely that this will prove to be the case.

There is left for consideration those red algæ which produce no tetraspores at any phase of their life history. They include a number of well-known types such as *Nemalion, Batrachosper-*

[11] Kuckuck, P., "Ueber *Platoma Bairdii* (Farl.) Kck.," *Wiss. Meeresuntersuch. Biol. Anstalt Helgoland.*, V, 187–203, 1912.

[12] Schiller, J., "Ueber Bau, Entwicklung, Keimung und Bedeutung der Parasporen der Ceramiaceen," *Oester. bot. Zeitsch.*, LXIII, 144, 203, 1913.

mum, Scinaia, Helminthora, etc., and at present constitute the field where research is most needed in connection with the life histories of the red algæ. Apart from asexual monospores the reproduction takes place only through carpospores produced in simple cystocarps. There are in the life histories no groups of tetrad cells to suggest the position of reduction divisions which explains the reasons why our understanding of alternation of generation in the *Rhodophyceæ* has come chiefly through higher forms exhibiting the tetrasporic phase. The first cytological research on a life history among the forms lacking tetraspores was the study by Wolfe[13] of *Nemalion.* This investigation brought out a number of important discoveries: the presence of a nucleus in the trichogyne, the mitosis which gives two sperm nuclei after the fusion with the trichogyne, the proliferation of the cells terminating the sporogenous filaments of the cystocarp to form successive carpospore mother cells, the structure of the chromatophore. With respect to the chromosome count in the life history Wolfe concluded that vegetative mitoses presented about 8 chromosomes and that 16 is probably the number shown by the mitoses in the developing cystocarp. The period of chromosome reduction was placed in the terminal cells of mature sporogenous filaments, one of the daughter nuclei, following a reduction mitosis, passing into a carpospore mother cell. The other reduced daughter nucleus was assumed to become established in the cell from which successive carpospores are produced by proliferation. The cytology of *Nemalion* is admittedly difficult and in the absence of a conspicuous group of four nuclei characteristic of reduction divisions (such as is found in the tetraspore mother cell) it is natural that critics of Wolfe's conclusions should have suggested other possible positions in the life history for the critical period of chromosome reduction. Thus it was suggested that reduction might take place at the germination of the carpospore, but Lewis[14] in a short note reports that the first and later mitoses in the sporelings are vegetative mitoses with about 8 chromosomes. A second possibility, that reduction takes place in the first division of the zygote nucleus in the fertilized carpogonium, is strongly debated by Svedelius in his recent paper on *Scinaia.*

[13] Wolfe, J. J., "Cytological Studies on *Nemalion,*" *Ann. of Bot.,* XVIII, 607–630, 1904.

[14] Lewis, I. F., "The Germination of the Spore of *Nemalion multifidum,*" *Science,* XXXV, 154, 1912.

Svedelius[15] gives a cytological study of *Scinaia furcellata* which suggests some fundamental readjustments of our conception of the cystocarp in those red algæ which lack the tetrasporic phase in their life histories. Monosporangia and spermatangia occur on the same plants growing out of and becoming cut off from mother cells at the surface of the thallus with evidence that successive crops may be formed from the same mother cells. Both monosporangium and spermatangium have a nucleus with about 10 chromosomes and the similarity of their structure and manner of development indicates that they are homologous organs. The 3-celled carpogonial branch requires a somewhat detailed account since its history presents phases not previously described for the red algæ. The terminal cell becomes the carpogonium and a mitosis gives a nucleus to the trichogyne as has been described for *Batrachospermum, Nemalion, Polysiphonia, Rhodomela, Delesseria* and *Griffithsia*. From the second or hypogenous cell is formed a group of 4 auxiliary cells rich in protoplasmic contents. The third or basal cell of the carpogonial branch develops finally the envelope of the cystocarp. The nuclei of the carpogonial branch including the female gamete nucleus in the carpogonium have 10 chromosomes which is the haploid number of the *Scinaia* plant. After the fertilization of the carpogonium the zygote nucleus, with 20 chromosomes, and consequently diploid, passes into one of the auxiliary cells which have become more or less fused together. In the auxiliary cell the large zygote nucleus prepares for and passes through a heterotypic mitosis with apparently clear evidence of diakinesis shown in the presence of 10 pairs of chromosomes. A second mitosis gives the tetrad of 4 nuclei but only one of these becomes concerned with the development of the gonimoblasts, passing back into the carpogonium from which the gonimoblasts arise. The other 3 homologous nuclei of the tetrad together with the nuclei of the auxiliary cells take no further part in the history of the cystocarp. Nuclei of the gonimoblasts have 10 chromosomes and this number is passed to the carpospores which are formed successively in rows; some of the gonimoblasts remain sterile and develop into long filaments resembling paraphyses.

A most unexpected outlook upon the life histories of the red algæ will be opened if these conclusions of Svedelius on *Scinaia* are confirmed and if studies on *Nemalion, Batrachospermum*, etc.,

[15] Svedelius, N., "Zytologisch-Entwicklungsgeschichtliche Studien über *Scinaia furcellata*," *Nov. Act. Reg. Soc. Scien. Upsal.*, IV, No. 4, 1915.

should also determine the position of chromosome reduction to be at the first mitosis of the zygote nucleus. The cystocarps of these plants would then be interpreted not as a diploid sporophyte generation but as a special haploid phase and the carpospores would have the same value as monospores. There would be no antithetic alternation of generations in such forms of the red algæ. Svedelius proposes the term *haplobiontic* for red algæ with this type of life history to be contrasted with *diplobiontic* forms (*Polysiphonia, Rhodomela, Griffithsia,* and *Delesseria*) where the gonimoblasts have been shown to be diploid in character and chromosome reduction finds its place in the terasporangia of an asexual generation. The diplobiontic type of life history is naturally conceived by Svedelius to arise from the haplobiontic by a delaying of the reduction divisions so that gonimoblasts carry forward the diploid number of chromosomes to the carpospores. The carpospores being diploid develop an asexual generation and their diploid sporangia becoming the seat of the reduction divisions take the characters of tetrasporangia, a new type of reproductive organ. The occasional suppression of reduction divisions in the tetrasporangium may be expected at times to transform this cell to a monosporangium, as in *Nitophyllum,* showing close analogies between the two structures.

In connection with the conclusions of Svedelius on *Scinaia* it should be remembered that Allen has placed the reduction period in the life history of *Coleochæte* at the first mitosis of its zygote nucleus. If this view is correct the cellular body developed in the oospore of *Coleochæte,* preliminary to the formation of a crop of zoospores, is a special haploid structure and may be compared with the gonimoblastic development in *Scinaia* as interpreted by Svedelius. The haplobiotic red algæ of Svedelius then, if clearly established, would have the same type of life history as *Coleochæte* and bearing in mind the resemblance of the young oogonium of *Coleochæte* to a carpogonium and trichogyne, the resemblance of its antheridia to a cluster of spermatangia and the branched filamentous structure of its thallus, the view that *Coleochæte* represents a type from which the red algæ might have arisen takes on added strength.

It is interesting to note how far removed from the theories of Schmitz and Oltmanns are the more recent interpretations of the life histories in the red algæ. The secondary or double fertilization assumed by Schmitz as an explanation of the union of ooblastema filaments with auxiliary cells was discredited by Olt-

manns's work and has received no support from the cytological studies of Yamanouchi, Lewis, Kylin and Svedelius. Oltmanns's view that tetraspores have no fixed place in ontogeny and are without relation to a sporophyte generation has been overwhelmed by the cytological work of the authors mentioned above. And now Svedelius argues that even the old view that cystocarps represent a sporophytic phase can not be correct for a group of the red algæ which he terms haplobiotic. The situation as it now stands may be summarized as follows: An antithetic alternation of generations may be expected wherever tetrasporic plants are found in a life history and in these forms the gonimoblasts also constitute a phase of the sporophyte. There is no sporophyte in the "haplobiotic" red algæ (*e. g.*, *Scinaia* with *Nemalion, Batrachospermum,* etc., not yet studied from this standpoint) and the gonimoblasts of these forms represent a haploid development of the zygote in position upon the plant, carpospores being equivalent to monospores. Fusions with auxiliary cells are merely cytoplasmic in character and associated simply with nutritive functions. The diplobiotic red algæ have come from the haplobiotic, which, carrying forward the reduction divisions through the gonimoblasts and carpospores to a new generation, the tetrasporic plants, have established the reduction divisions in the tetrasporangium. In theory these views are simple and logical. For the antithetic alternation of sexual and tetrasporic plants the evidence is considerable and convincing. What will be the conclusions for the "haplobiotic" types? Will future studies establish their existence?

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